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Optimal Survey Design: Lessons from a Stratified Random Sample of Macrobenthos

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CUFF, W., AND N. COLEMAN. 1979. Optimal survey design: lessons from a stratified random sample of macrobenthos. J. Fish. Res. Board Can. 36: 351–361.

A stratified random sample of macrobenthos in Western Port (Victoria, Australia) provided adequate data to take an a posteriori look at the efficiency of various random survey designs in terms of their ability to provide precise estimates of the mean number of individuals per taxon, i.e. mean estimates with the smallest possible variance. Emphasis was placed on the efficiency of the stratified simple random sampling design. The analyses showed that bay-wide estimates resulting from various stratified designs would not have been substantially more precise than those from simple random sampling. This conclusion was not influenced by the allocation strategy used in the stratified design. On the other hand, substantial gains in precision could have been made, *for the same total number of grab samples*, by increasing the number of stations at the expense of the number of grab samples per station. Our data suggested that the optimal number of grab samples per station is only one, contrary to the common practice of multiple grab samples per station.

Key words: stratified, random, survey, optimal, macrobenthos, sample, Western Port

CUFF, W., AND N. COLEMAN. 1979. Optimal survey design: lessons from a stratified random sample of macrobenthos. J. Fish. Res. Board Can. 36: 351–361.

Un échantillon aléatoire stratifié de macrobenthos prélevé dans la baie Western Port (Victoria, Australie) a fourni des données qui ont permis d'examiner *a posteriori* l'efficacité de divers plans de relevés aléatoires et leur aptitude à fournir des estimations précises du nombre moyen de sujets par taxon, i.e. des estimations moyennes avec variance aussi petite que possible. On a mis l'accent sur l'efficacité des plans d'échantillonnage simple stratifié. Les analyses démontrent que les estimations obtenues à la grandeur de la baie à partir de divers échantillonnages stratifiés n'auraient pas été beaucoup plus précises que celles obtenues par un

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échantillonnage aléatoire simple. Cette conclusion n'est pas influencée par la stratégie d'allocation employée dans le plan d'échantillonnage stratifié. Par ailleurs, on pourrait obtenir une précision notablement plus grande, *pour le même nombre total d'échantillons prélevés à la benne*, en augmentant le nombre de stations au dépens du nombre d'échantillons prélevés à la benne par station. Nos données suggèrent que le nombre optimal d'échantillons prélevés à la benne par station est seulement un, contrairement à la pratique commune de prélever plusieurs échantillons par station.

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BOTH random and nonrandom survey designs can be found in the benthic literature. An advantage of the random survey design is that it provides both unbiased mean and variance estimates (Greig-Smith 1964). But the acceptability of the random design has been limited by the belief that it requires impracticably large sample sizes (e.g. Holme 1964; McIntyre 1971; King 1971; Clifford and Stephenson 1975).

A recent paper by Saila et al. (1976) considered in some detail optimal survey design for random sampling of benthos in the New York Bight. The authors concluded that an inordinate number of randomly chosen samples is not needed for making reasonable tests of hypotheses or inferences about the relative abundance or community structure of selected macroinvertebrate species. They suggested the utility of stratified sampling. It thus seems useful to direct further effort towards finding efficient random designs.

There exist to date very few examples of random surveys of benthos and hence virtually no guidelines as to the relative efficiencies of the various random designs. Guidelines based on actual random survey experience will follow only after a number of such surveys have been conducted. But it may be possible to shorten this search time by using data obtained from random surveys as they are conducted to calculate the expected efficiencies of various random survey designs for the specific study areas. Such calculations should be capable of generating tentative suggestions about optimal survey designs that can be used and tested for general relevance in future surveys.

As part of the Westernport Bay Environmental Study (Shapiro 1975) we conducted a stratified simple random sample of the macrobenthos of Western Port (Fig. 1). The survey results are described in Coleman et al. (1978). The objective of the present study was to use the data from our random survey to take an a posteriori look at the expected efficiency of various random designs in Western Port. Within-stratum variance estimates from our survey were used to calculate the expected variances of the universe (i.e. bay-wide) mean estimates assuming a variety of random survey designs. The variety of analytical techniques used are all part of survey statistical methodology (e.g. Cochran 1963; Som 1973) but a number of them have not yet been used in benthic ecology. It was thus felt necessary for

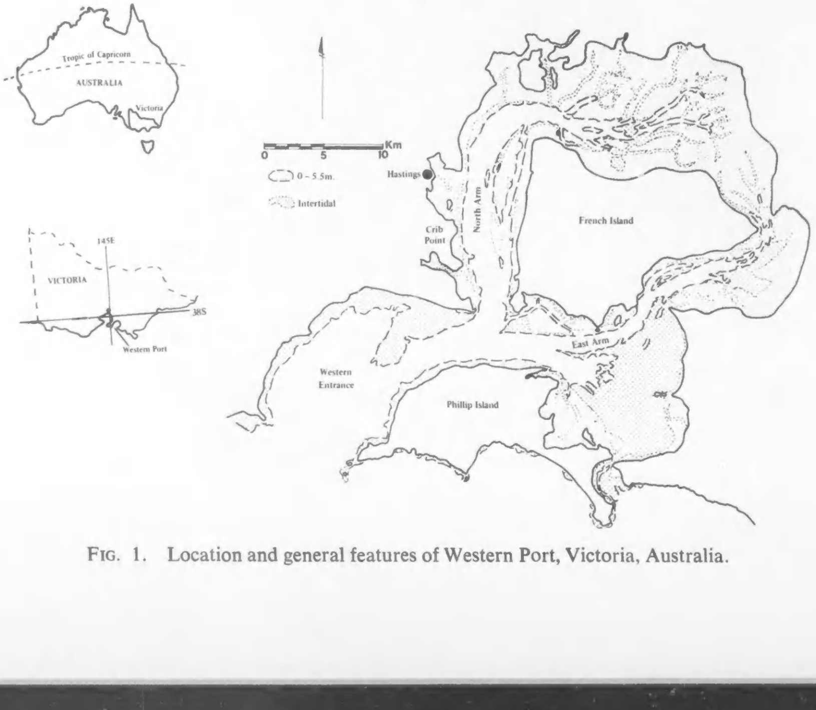

FIG. 1. Location and general features of Western Port, Victoria, Australia.

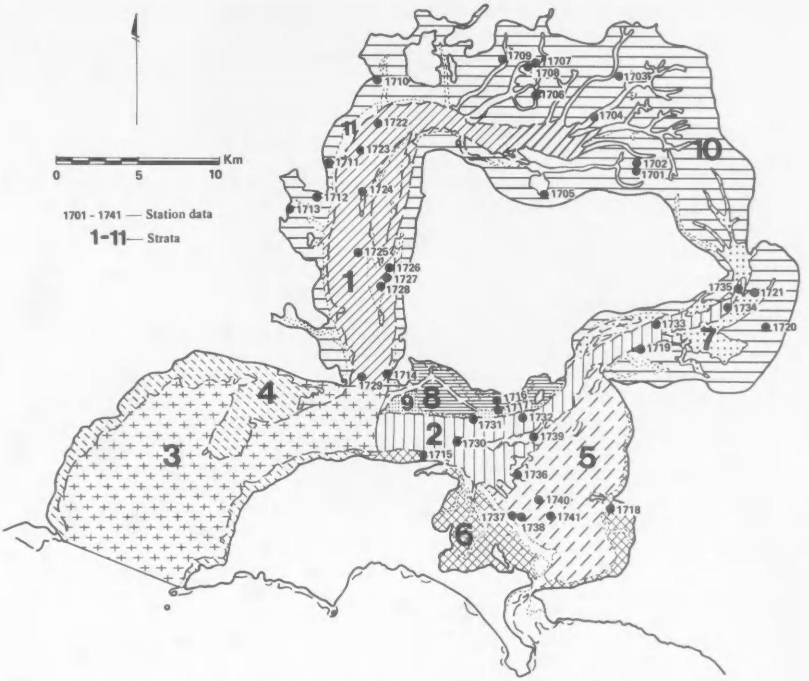

FIG. 2. Strata defined and stations sampled in the survey of Western Port. Stations 1722–1729 are located in stratum 1, 1730–1733 in stratum 2, 1736–1741 in stratum 5, 1715 and 1718 in stratum 6, 1734–1735 in stratum 7, 1716–1717 in stratum 8, and 1701–1714 and 1719–1721 in stratum 10.

the clarity of this paper to apply the techniques to a limited number of variables.

In Western Port relatively few of the species provide the majority of the individuals (Coleman et al. 1978) and so the use of these dominant species seemed initially to be an obvious choice of variables. Of 273 crustacean species only 3 were dominant; of 204 polychaete species only 6 were dominant; and of 59 mollusc species 9 were dominant. While these 18 species represent a substantial reduction over the potential number of variables (572 species), we felt that in relation to the variety of analyses conducted, this number of variables was still too large. Thus a smaller set of three variables was used: the number of crustaceans, of polychaetes, and of mollusc individuals per station. These variables are more highly aggregated taxonomically than one may like. On the other hand, they avoid the important disadvantage of null values at some stations. They are thus, perhaps, suitable for a first application of the methodology introduced here.

Methods

SURVEY DESIGN AND IMPLEMENTATION

The survey design was stratified simple random sampling with proportional allocation of sample size to different strata (Som 1973). Stratification was used to get regional as well as universe estimates, simple random sampling (srs) within strata because it was easy to implement, and proportional allocation because the relative sizes of the strata could be determined from a map.

Eleven strata were defined (Fig. 2) but as sampling effort was limited by time and labor considerations to 41 stations we decided to eliminate strata 3 and 4 from the universe definition. When sampling effort was allocated proportionally to the remaining strata, strata 9 and 11 were each allocated less than one station and rounded off to zero. The predicted sample sizes for the other strata were also rounded off and one station from stratum 6 given to stratum 8 to bring the latter's station count to 2 stations. The resultant allocation is given in Table 1 (n_h: number, n, of stations in stratum h).

Stations (Fig. 2) were chosen at random from an enlargement of a photographic Extract of Admiralty Chart 1707. Stratum boundaries were identified on the map and each stratum was subdivided into a set of 1-mm² areas, corresponding to areas in the field of 60 × 60 m. For each stratum, the square millimetre areas on the map were numbered and a table of random numbers used to select the station positions. The stations marked on the map were located, with the use of shipborne radar, with a maximum discrepancy of 30 m. At each station three 0.1 m² Smith–McIntyre grab samples (Smith and McIntyre 1954) were

TABLE 1. Numbers of elementary units, sample units, and sampling costs per stratum. The symbols are explained in the text.

	Elementary and sampling units			Costs (1973 A$)		
					c_{2h}	
Stratum	N_h* 10^{-8}	n_h	K_h* 10^{-6}	c_{1h}	field	lab & field
1	2.77	8	14.9	2.30	0.20	7.00
2	1.32	4	7.1	2.50	0.20	7.00
5	1.88	6	10.1	3.60	0.20	7.00
6	1.05	2	5.7	4.40	0.50	7.30
7	0.58	2	3.1	6.30	0.20	7.00
8	0.53	2	2.8	3.20	0.50	7.30
10	6.39	17	34.4	5.40	0.50	7.30

taken. The three grabs were usually collected within about 15 min while the boat was swinging at anchor.

Further details on survey design and implementation are in Coleman et al. (1978).

DATA ANALYSIS

The data can be analyzed as either a stratified single-stage or a stratified two-stage srs (Som 1973). It seems reasonable, for example, to visualize stations as first-stage units and grab samples as second-stage units in a two-stage design. This design would, however, require a randomly based selection of grab samples at a station but we had no way of accurately fixing the boat over a specific location of bottom, or of predicting its drift pattern. The best that could have been achieved was a haphazard selection, not necessarily the same as a random selection. It thus also seems reasonable to analyze the data as a single-stage design with data from the three grabs pooled before analysis. Analyses were conducted for both the single- and two-stage designs.

In the single-stage design the universe is considered to be divided into $L(=7)$ strata with stratum h having N_h stations, or elementary units (Table 1), each of an area equal to the sum of the 3 grab samples/station, i.e. 0.3 m^2. From the N_h elementary units a sample of n_h sample units were selected at random (Table 1). The study variable, denoted as y_{hi}, is the total number of individuals in the three grabs of the ith station in the hth stratum. Calculations included the average y_{hi} per station with variance of the estimator and the 95% confidence limits of the universe station-average estimates, using the effective degrees of freedom for the t-statistic (Cochran 1963).

In the two-stage design the universe is considered to be divided into $L(=7)$ strata with the hth stratum having K_h first-stage units, or fsu's; each fsu represents the area through which the sampling vessel moved while the three grabs were being taken. The fsu area was calculated for each station by assuming a circumferential swing of 30° of the boat around the anchor, with a 1-m movement at right angles to the swing trajectory. These calculations suggested an average fsu area of 5.6 m^2 (SD = 3.3 m^2). The total number of fsu's per stratum (K_h) is given in Table 1. From the K_h fsu's a sample of k_h sample fsu's were selected at random. (The k_h's are identical in number to the n_h's of the single-stage design, Table 1.)

The ith sample fsu contains M_{hi} second-stage units, or ssu's ($M_{hi} = 56$). Each ssu represents the 0.1 m^2 Smith–McIntyre grab sample. From the M_{hi} ssu's a sample of m_{hi} sample ssu's (=3) were selected haphazardly. The study variable, now denoted as y_{hij}, is the number of individuals in the jth grab sample in the ith station in the hth stratum. Calculations included the average y_{hij} per fsu with variance of the estimate.

The optimal number of ssu's in a two-stage design — applicable to minimum variance at fixed cost or vice versa — was calculated separately for each stratum, h, according to Som (1973) as

$$\sqrt{V_{2h}c_{1h}/(V_{1h}c_{2h})}$$

where c_{1h} is the variable cost per fsu and c_{2h} is the variable cost per ssu. The fsu cost is calculated as the product of crew costs per unit time (1973 Australian dollars) and cruising time (c_{1h}, Table 1). The field component of ssu cost was calculated as the product of crew costs and sampling time (c_{2h} field, Table 1); the laboratory component was estimated at 1973 A$6.80/grab and is given in combination with the ssu field costs in Table 1 (c_{2h} lab & field).

The variance V_{2h} is the variance within the fsu's and V_{1h} is the variance among the fsu's. The estimate of V_{2h} was calculated as the error MS of a one-way analysis of variance with fsu's (stations) as treatments and ssu's (grab samples) as replicates. The estimate of the among-fsu variance V_{1h} was calculated as the per-ssu average of the difference between the group MS and the error MS (Som 1973).

The effect of alternative designs on the size of the resultant universe variance estimates was investigated. Firstly, a poststratification (Som 1973) was conducted on the basis of a numerical classification (Clifford and Stephenson 1975) of the data (Coleman et al. 1978). In this analysis three strata were defined. The two major strata represent the sublittoral channel areas (strata 1, 2, and 7), and tidal flat/shallow sublittoral areas (strata 5, 6, 8, and 10). A third and minor stratum located near Hastings in the North Arm (Fig. 1), consists solely of stations 1711, 1712, and 1713 (Fig. 2).

Secondly, the expected variances of the universe mean under each of equal, proportional, optimal, and Neyman allocation were calculated. (The strict validity of this procedure depends on the correctness of the within-stratum variance estimates obtained from our survey.) The ex-

TABLE 2. Universe estimates (no./0.3 m^2) of polychaetes, crustaceans, and molluscs from a stratified single-stage srs analysis with proportional allocation. The effective degrees of freedom (Cochran 1963) used were 4 for polychaetes, 12 for crustaceans, and 7 for molluscs.

Taxon	Mean	95% Confidence limits
Polychaeta	157.2	90.6–272.9
Crustacea	91.9	62.3–135.4
Mollusca	15.0	8.2–27.5

pected variances were calculated under a single-stage design and estimates of variable cost per station were needed for optimal allocation. These were calculated as the sum of the fsu cost (c_{1h}, Table 1) and 3 times the ssu cost (c_{2h} lab & field, Table 1). The results were compared to the expected variance estimates from an srs design (Cochran 1963).

A final type of analysis involved studying the relationships between Neyman allocations for each of a number of variables. The Neyman allocations were for minimum variance, assuming fixed sample size (Som 1973). A simple search was then made of the effects of some possible compromise allocations.

Results

INITIAL ANALYSES

The frequency distributions of the data (number of individuals per station for each of polychaetes, crustaceans, and molluscs) were skewed to the right but a log transform removed the significant skewness. The following analyses were thus performed on log transformed data.

The universe estimates of individuals per taxon, per station, from a stratified single-stage srs with proportional allocation are shown in Table 2. There is an (geometric) average of 157 polychaetes, 92 crustaceans, and 15 molluscs/station in Western Port. The universe mean and variance estimates from a two-stage design were virtually identical to those obtained from the single-stage analysis of Table 2. No difference in variance was noted for polychaetes, while there was only a 0.1% increase for each of crustaceans and molluscs. The reason for the lack of difference between the one- and two-stage designs is discussed in Appendix 1.

The predicted optimal number of ssu's per fsu in a two-stage design is small (Table 3). (The table gives the estimated optimal ssu's for only polychaetes and crustaceans in the larger strata. The mollusc data contained many zero samples making the calculations unreliable.) The most generous results, using field ssu cost estimates (c_{2h} field, Table 1), suggested 2–5 ssu's/fsu. The more complete calculations, using both laboratory and field ssu cost estimates, suggested only 1 ssu. A similar conclusion follows from ignoring costs and concentrating solely on the relative magnitudes of the among- and within-station (fsu) variance estimates (Table 3).

Various designs can be compared by using the concept of "precision," defined in terms of sampling variances, s^2, as follows: the precision of a mean estimator from one design (t) relative to another (k) is s^2_k/s^2_t (Som 1973). The precision of the universe estimates from a stratified one-stage design relative to srs were 0.78 for polychaetes, 0.88 for crustaceans, and 0.74 for molluscs. Stratification did not produce the desired increase in precision. In the following section the expected precisions of various other designs are calculated in an attempt to find a more efficient design than srs for sampling Western Port benthos.

EFFECT OF ALTERNATIVE DESIGNS ON PRECISION

Poststratification — Earlier analysis (Coleman et al. 1978) suggested that the stations fell naturally into two main faunal assembleges and one minor one. A poststratification (Som 1973) was conducted on the basis of the sampled stations. The resultant universe estimates suggested a precision of the poststratified analysis

TABLE 3. Optimal number of second-stage units per first-stage unit (ssu's/fsu) for a stratified two-stage srs design, with among-(V_{1h}) and within-station (V_{2h}) variance estimates.

			Optimal number ssu's/fsu		
Stratum	V_{2h}	V_{1h}	not costed	field costs	lab & field costs
			Polychaeta		
1	0.4483	0.5148	0.93	2.98	0.53
2	1.1413	2.7878	0.64	2.20	0.38
5	0.2650	1.3723	0.44	1.69	0.31
10	0.3030	0.4214	0.85	2.80	0.72
			Crustacea		
1	0.7837	0.8693	0.95	3.04	0.54
2	0.2980	1.5261	0.44	1.52	0.26
5	0.5415	0.3322	1.28	4.92	0.91
10	0.4261	1.2551	0.58	1.93	0.50

TABLE 4. Estimates of the coefficients of variation (C.V.) of the logged universe means under four allocation schemes for stratified single-stage srs (equal, proportional, optimal, Neyman allocation) and for srs. Logged means for polychaetes, crustaceans, and molluscs were 2.197, 1.963, and 1.177, respectively.

Taxon	srs	Equal	Proportional	Optimal	Neyman
Polychaeta	3.5	3.8	4.0	3.3	3.3
Crustacea	3.7	5.1	3.9	3.6	3.6
Mollusca	8.1	11.5	9.5	8.5	8.5

relative to the initial one-stage analysis of 1.31 for polychaetes, 1.14 for crustaceans, and 1.20 for molluscs. Precisions of the poststratified analysis relative to srs were 1.02 for polychaetes, 1.00 for crustaceans, and 0.89 for molluscs.

Allocation strategy — The estimates of the within-stratum variances from the (initial) stratified single-stage srs analysis allowed a tentative comparison of the universe variance estimates produced by proportional allocation to those estimates that would have been produced had any of equal, optimal, or Neyman allocation been used. (Neyman allocation is used here in the sense of optimal allocation with the variable cost per station assumed equal for each stratum; Som 1973.) The calculated C.V.s of the universe means for each allocation strategy — as well as for srs — are given in Table 4.

As expected, our analyses show that the optimal allocation strategy — Neyman allocation being a special form of it — would have produced the most precise variance estimates (Table 4). Precision estimates relative to proportional allocation of 1.47, 1.21, and 1.26 were produced for polychaetes, crustaceans, and molluscs, respectively; and relative to srs were 1.14, 1.06, and 0.93, respectively. The nature of the C.V. differences between each of proportional and optimal allocation, and srs are elaborated in detail in Appendix 2.

COMPROMISE ALLOCATIONS

The analyses presented above, in terms of the initial and alternative designs, suggested that a stratified single-stage srs, with Neyman allocation of stations to strata, would have given the smallest variance estimates. (Later we discuss the significance of the precision gains afforded by Neyman allocation.) By assuming such a design and using the within-stratum variance estimates, we calculated the optimal sample sizes per stratum. The results for each of polychaetes, crustaceans, and molluscs — calculated separately — show that the optimal distribution of available sampling effort varies with taxonomic group (Table 5, legend). It thus is desirable to try to find a compromise allocation that simultaneously maximizes the precision of each variable.

TABLE 5. Various compromise allocations. The rounded Neyman estimates for noncompromised sample sizes per stratum ($n = 41$) were

Polychaeta 5, 5, 6, 8, 3, 1, 13
Crustacea 8, 5, 3, 5, 0, 1, 19
Mollusca 7, 2, 6, 6, 1, 1, 18.

	Precisions relative to srs		
Compromise allocation	Polychaeta	Crustacea	Mollusca
Average			
7, 4, 5, 6, 1, 1, 17	1.00	1.01	0.88
from 7, 8, to 10			
7, 4, 5, 6, 0, 0, 19	1.07	0.92	0.86
from 7, 8, to 6			
7, 4, 5, 8, 0, 0, 17	1.11	0.89	0.85
from 10 to 7, 8			
7, 4, 5, 6, 2, 2, 15	1.06	0.95	0.87
from 6 to 7, 8			
7, 4, 5, 4, 2, 2, 17	0.99	0.97	0.86

Various modifications (Table 5) of the average allocation failed to find any obviously preferable compromise. The compromise that allocated sampling effort from strata 7 and 8 to stratum 6 did well for polychaetes but poorly for crustaceans. The average compromise gave the highest precision value for crustaceans but a relatively low value for polychaetes. No compromise resulted in a substantial change in mollusc precision.

Discussion

EFFICIENCY OF THE STRATIFIED DESIGN

The above analyses did not uncover any stratified design that would have produced substantially more precise estimates than srs. The most precise stratified design would have produced pre[illegible]ns relative to srs of only 1.14, 1.06, and 0.93 for polychaetes, crustaceans, and molluscs respectively. (These precision estimates may not be as accurate as one might like. To get good universe estimates for any allocation strategy, it is first necessary to obtain good estimates of within-stratum variances. In our survey, strata 6, 7, and 8 were each sampled by only 2 stations, too small a number to ensure good estimates of within-stratum variances.) But even if the precisions are only roughly correct, it is still possible to say that in many applications gains of this magnitude would not be worth the effort of obtaining presurvey estimates of within-stratum variance, and especially not so if compromise allocations were required; Table 5 shows that shifting of even a small number of stations between strata can result in nontrivial changes in precision. In these cases srs would be the preferred design.

A stratified design will, nevertheless, be preferred in many instances. Stratification can be used to sample along environmental gradients (McIntyre 1971; Holland et al. 1977). Also, stratification can be used to restrict sampling effort in various ways, allowing unbiased regional as well as universe estimates. This is an advantage in Western Port where future development is likely to be regional; and unbiased, precise regional estimates are necessary if any attempt is to be made to determine the effects of development.

Where it is reasonable to choose a stratified design, then optimal allocation will be chosen where maximum precision is critical; but then it will be desirable to restrict the number of strata to a set on which it is possible to get good presurvey estimates of within-stratum variances. In Western Port, for example, optimal allocation would be less effectively applied to the stratification actually used than to that suggested by a numerical classification of the data (Coleman et al. 1978); viz., three strata consisting of the channel areas, the tidal flat/shallow sublittoral areas, and a smaller area of unique faunal composition. This said, the advantage of optimal over proportional allocation may not be large (Table 4). (The poststratified analysis showed that proportional allocation can produce universe estimates of about the same precision as srs.) And proportional allocation has the advantage of not requiring within-stratum variance or cost information. Thus we, and others (e.g. Abramson 1968; Russell 1972), used proportional allocation.

OPTIMAL NUMBER OF GRAB SAMPLES PER STATION

Our analyses (Table 3) suggested that the most precise universe estimates can be obtained by taking only one grab sample at each station. This conclusion was reached when both laboratory and field costs were used, as well as when only variance information was used in the calculations. From 2–5 grab samples/station were suggested when laboratory costs were ignored, pointing to the importance of clearly incorporating the costs associated with sorting, identification, and counting of the animals in the laboratory.

Saila et al. (1976) also considered the question of optimal numbers of grab samples per station, for each of a number of selected species. They found that it was optimal to choose 1 grab sample/station for each of four benthic species (*Nucula proxima*, *Prionospio malmgreni*, *Spiophanus bombyx*, *Tharyx acutis*), 2 grab samples/station for each of two species (*Cossura longocirrata*, *Paraonis gracilis*) and 3 grab samples/station for *Cerianthus americanus*. They used dynamic programming to minimize a cost function subject to a precision constraint. The cost function used was

$$c_1n_1 + c_2n_1n_2$$

where n_1 is the number of sample fsu's and n_2 is the number of sample ssu's per fsu. They estimated that it costs "about $25 to collect a Smith–McIntyre sample whether the samples are repeated within a station or within a stratum." They also stated that it costs "about $300.00 to sort and analyze each sample for relevant taxa." Then, as a first approximation they estimated a "cost of $325.00 for acquisition and analysis of each sample, regardless of origin"; the costs per fsu (c_1) and per ssu (c_2) were then assumed to be identically equal to $325.

When combined with these cost estimates, their cost function seems to incorrectly count stations twice. Each sample is said to cost $325 for its acquisition and analysis, and since the total number of samples is n_1n_2, the total cost should be $\$325n_1n_2$. The purpose of the first term (c_1n_1) is thus unclear. In our analysis we used the same form of cost function as Saila et al. (1976) but we let the c_1 cost reflect only the personnel costs of cruising to a station (c_{1h}, Table 1) while the c_2 cost reflected both laboratory effort and field sampling effort (c_{2h} field & lab, Table 1). A similar costing schedule has been used by Abramson (1968). Had Saila et al. (1976) used these definitions their c_1 estimate would have been roughly $25 and their c_2 estimate roughly $300, and their estimated ssu's per fsu would have been smaller than noted above. Thus the analyses of Saila et al. (1976) lend support to our conclusion that it is optimal to take only one grab sample at each station. This is interesting because Saila et al. (1976) conducted their analyses using data from each of a number of species considered separately, while we used data from highly aggregated species complexes.

Both the study by Saila et al. (1976) and our study approached the determination of optimal number of grab samples per station using standard survey statistical techniques. These techniques assume that the objective of a survey is either to obtain a minimum universe variance under a maximum allowable cost constraint or to spend minimum money to get universe mean estimates with a maximum allowable variance. These objectives do not cover all the objectives McIntyre (1971) has noted for quantitative benthic sampling: "to enable valid statements to be made about the number of species present and about the distribution and density (number of individuals and/or biomass per unit area) of the fauna." The objectives assumed by survey statistics, and hence by this study, relate most closely to McIntyre's (1971) objective of making valid statements about the density (number of individuals per unit area) of the fauna.

McIntyre (1971) suggested, largely on the basis of Longhurst's (1959) work, that 5 grab samples/station with a 0.1-m^2 grab should be regarded as a minimum requirement. This should give "adequate information about the density . . . of the abundant species" (Longhurst 1959). This conclusion was based on a plot of the abundance of recruited species as a function of the number of samples taken at a station. Longhurst (1959) noted that for the abundant species there were no significant differences between the mean number of individuals per grab for the complete 10 samples (1 m^2) and for the first 5 samples (0.5 m^2); and that there was no trend in the cumulative means of the abundant species plotted over the whole sample. Thus the "adequate information" referred to above seems to be that the mean number of individuals per sample would not change substantially if more samples were taken at the station.

Longhurst's (1959) method of defining an adequate number of grab samples per station is based solely on variation among samples at a station. It does not balance the need to measure variation among samples at a station with the need to measure variation among stations. When the survey objectives relate to drawing inferences about an area larger than that implied by a "station," then this method leaves itself open to the possibility of wasting sampling effort through overdefining the stations. When McIntyre (1971) attempted to calculate the required number of stations to get a precise universe density estimate — assuming multiple grabs per station — he found that the suggested numbers were in excess of the available effort. He concluded that a high degree of precision "would require a very large number of samples." Considering the results of Saila et al. (1976) and of this study, an alternative explanation seems equally likely — that his stations were overdefined, and hence wasted sampling effort that could have been usefully applied to obtaining precise universe estimates within reasonable limits of laboratory effort. (Although it's not clear from his article McIntyre (1971) apparently summed the data from 3 grabs/station and assumed an srs design to estimate the number of stations required to obtain a sufficiently precise mean.)

Other studies have also suggested the desirability of taking multiple grabs at a station. Holme (1953) first used a plot of cumulative number of species as a function of the number of samples taken at a station to determine an adequate qualitative picture of the fauna at a station. The curve tends to saturate and the "minimal sampling area" (Holme 1964) is defined accordingly. Studies based on such a "cumulative curve" (Holme 1964) have tended to suggest from 3 (Lie 1968) to 5 grab samples/station (McIntyre 1971), although the exact number can vary substantially from one station to another (Gaufin et al. 1956; Harris 1957). The "cumulative-curve" method stresses the number of species present in a sample of a given size, without taking account of their abundance; this contrasts with Longhurst's (1959) "recruitment-curve" method (Holme 1964), mentioned above, which stresses the densities of the species taken. Yet the cumulative curve also measures only variation at a station and, depending on the point on the curve chosen to represent the "minimal sampling area," may give excessive emphasis to variation among samples at a station.

It is, however, possible that the cumulative-curve and the recruitment-curve methods are relevant to objectives other than density estimates. The other two objectives of a quantitative survey suggested by McIntyre (1971) are to enable valid statements about the distribution of the fauna and about the number of species present. The problem of determining optimal sampling designs for discovering distributional patterns over large areas has not received much attention. Stephenson et al. (1974) conducted some preliminary observations relating the number of grab samples per station to the intuitive acceptability of the patterns produced by the methods of numerical classification. Their observations suggested 25 grab samples/station, although they found this number impractical and used 5 grab samples/station in their survey. Gunnerson (1966) observed variations in spectral density peaks in relation to sampling strategies to determine the best sampling interval for uncovering patterns in the data. Finally, some general considerations may be found in Clifford and Stephenson (1975, p. 143–146) and in Bunce and Shaw (1973). But the value of the cumulative- and recruitment-curve methods is limited in terms of this objective, at present, because they have not been explicitly related to the detection of pattern in an area larger than that implied by a "station."

The cumulative-curve method has obvious usefulness for drawing valid conclusions about the number of species present. In an interesting example, Ursin (1960) extrapolated the cumulative curve to the universe area to estimate the total number of species present in the area. He used samples accumulated both at a station and from various stations throughout the sampled area in constructing the curves. Holme (1964) and Lie (1968) correctly point to the dangers of extrapolating far beyond the sampled range but, nevertheless, Ursin's (1960) estimates are not unreasonably different from previous estimates using other methods. Yet, in spite of the cumulative curve's usefulness in determining the number of species present, there remains the problem of balancing extra samples within the stations against more stations when the total sample size is fixed by time and labor constraints. At the moment there exists no empirical evidence to suggest that the species count in a homogeneous area (such as a stratum) will be any different for a fixed total sample size if one takes multiple grabs at a station than for a single grab per station, with more stations; yet the latter strategy has the added advantage of giving more precise universe density estimates.

The cumulative-curve method has its antecedents in plant ecology. During the three decades to 1950 plant ecologists had extensively debated the utility of cumulative curves, called species-area curves in plant ecology, and the characterization of "minimal areas" for quadrat size (reviewed by Greig-Smith 1964). Of three methods for obtaining data for constructing species-area curves, one involved adding the data from the appropriate number of small quadrats and this was the approach introduced to benthic ecology by Holme (1953). But two relevant difficulties have been pointed out with the species-area curve and the concept of "minimal area." Firstly, the practice of adding data from the appropriate number of small quadrats in constructing species-area curves was shown to be faulty. Greig-Smith (1964, p. 152) cites a study that shows that two aggregated species, confined to different parts of a local area so that they could occur together only in a very large "grab area," may be included in a quite small "station area." Secondly, he noted that no precise definition of "minimal area" had been formulated. We have contended above that the "minimal area" is best defined after a joint consideration of the within- and among-station variability. When it is not defined so, it is hard to see how to choose between various possible criteria of "minimal area": Holme (1953) used a visual inspection of the curve; Longhurst (1959) doubted the value of the cumulative curve in defining the minimal area and used the recruitment curve instead; even so Holme (1964) felt that both the cumulative-curve and recruitment-curve methods are useful; Gaufin et al. (1956) and Lie (1968) used the cumulative curve but defined the minimal area in terms of the number of grabs that are needed to collect a high percentage of the species collected in the series of samples. Unless an objective evaluation can be made of these various options, the "minimal area" concept will have only limited value.

OTHER WAYS OF OBTAINING PRECISE UNIVERSE ESTIMATES

The discussion to the present has concentrated on getting precise universe estimates by looking for the best survey design. But gains in precision can also be made by finding ways of reducing natural variation. McIntyre (1971) used variables of mean counts per grab of polychaete, crustacean, and mollusc abundance, noting that the spatial variation among such aggregated variables may be less than among species data. Longhurst (1959) also suggested the utility of gross faunal indices of total number of individuals in giving a quick, overall measure of density of the fauna in a particular area. Recently, Holland et al. (1977) found yearly changes in the numerically dominant species of macrobenthos and suggested the possible attractiveness of "summary measures of community structure," being total number of species, diversity indices, biomass, and total number of individuals. These authors have suggested the use of taxonomically aggregated variables for reasons such as the relative ease of obtaining them and their encompassing nature in addition to their relative stability. Where usefully applied such variables can produce gains in precision.

Our survey was one aspect of the Western port Bay Environmental Study and as such was subject to managerial directives to produce results that can be obtained relatively quickly and can be readily understood in the broad context inherent in environmental studies. One choice of variable that may relate to such directives is that used in this study: a highly taxonomically aggregated type. There are obvious limitations to aggregating many species into rather heterogeneous groups at the expense of other, perhaps more meaningful, characteristics such as feeding types, sediment preferences, environmental tolerances to salinity, temperature, and so on. Yet we believe that such taxonomically aggregated variables represent a logical starting point. From the broad framework supplied by the density estimates of each major taxonomic group, one can begin to discuss more specific aspects. (The methodology used in this study should be applicable to most variables.)

A second way by which one might reduce natural variation was suggested by Saila et al. (1976). They calculated the optimal number of grab samples per station and the optimal number of stations for each of a variety of selected species. On trying to find a compromise allocation between those given for the species considered separately, they found by dropping two species from the seven considered that they could reduce the required sample size by one half. This suggests that it may be useful to at least consider the implications involved in omitting variable species from the survey.

A third choice, theoretically attractive, involves taking a number of grab samples at a station but lumping them and taking a subsample for laboratory analysis. This "composite" sample should be more typical of the local area and hence help to reduce variation between stations. To get an unbiased random sample from a lumped sample one would either have to number each animal and select a subset of numbers at random or to ensure that the animals were distributed according to a Poisson distribution and choose a subsample from the lumped sample of substrate plus animals. The first alternative is feasible but time consuming; the latter alternative may present practical problems in getting the animals distributed in the substrate according to a Poisson distribution. It is interesting, however, that a rocking-chair dredge does in fact operate in such a manner as to produce a type of "composite" sample (Saila et al. 1965). The dredge rocks back and forth on skid pads, alternately withdrawing the teeth from the sediment to effectively integrate the small-scale cells of contagion (Russell 1972).

THE LESSONS

The main lessons to be drawn from our survey data are that no random survey design is likely to produce substantially more precise universe estimates than any other; and that *for fixed overall number of samples*, the greatest amount of precision can be obtained by having only a single grab sample per station, allowing more station effort.

The second lesson is based on an expression that is a function of the ratios of each of the per fsu to per ssu variable costs and the within- to among-fsu variances. Laboratory costs are always high in benthic surveys and this fact, by itself, will tend to reduce the predicted optimal number of ssu's per fsu. In Western Port the within-fsu variance estimate was usually a bit smaller than the among-fsu variance estimate (Table 3); thus considerations on variance data alone suggested only 1 grab/station. More generally it is known (McIntyre 1971) that many benthic populations show contagious distributions. If the contagion is small scaled — relative to the station area — then the within-fsu variance will be quite large, perhaps approaching the between-fsu variance. And in such a case the predicted optimal number of ssu's per fsu will, on variance considerations alone, again be one.

Most benthic surveys are interested in satisfying a variety of objectives. It is not possible to say how far the lessons of our study will carry over to objectives other than to obtaining precise universe estimates. But the essential trade-off will always be there: intense sampling of a local area with few stations overall vs. minimal sampling at a local area with more stations overall. Our analyses suggest the latter as the better strategy.

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Appendix 1

The explanation for the lack of difference in the estimates between the single- and two-stage designs can be best seen from the formula for the variance of the universe total estimator, for a two-stage design (Yamane 1967):

$$\sum^{L} \frac{K^2{}_h}{k_h} V_h + \sum^{L} \frac{K_h}{k_h} \sum^{k_h} \frac{M^2{}_{hi}}{m_{hi}} V_{hi}$$

TABLE A1. Percentage of total variation attributable to stations (fsu's) within strata, and grab samples (ssu's) within stations for each of polychaetes, crustaceans, and molluscs.

	Percentage of variation due to	
Taxon	Stations (fsu's)	Samples (ssu's)
Polychaeta	72	28
Crustacea	64	36
Mollusca	70	30

where V_h is a measure of the variation among the fsu's in the hth ($h = 1, 2, \ldots, L$) stratum; V_{hi} is a measure of the variation among the ssu's within the ith ($i = 1, 2, \ldots, k_h$) fsu in the hth stratum; K_h is the total number of fsu's in the hth stratum from which a sample of k_h sample fsu's are selected at random; and M_{hi} is the total number of ssu's in the ith fsu and the hth stratum from which a sample of m_{hi} sample units is selected at random. In this equation the variance weighting coefficient is much larger for V_h than for V_{hi}. For stratum 10, for example, K^2_{10}/k_{10} is more than 3 orders of magnitude larger than

$$\frac{K_{10}}{k_{10}} \sum^{k_{10}} \frac{M^2_{10,i}}{m_{10,i}}.$$

The universe variance estimator of the single-stage design is based on variation among stations (i.e. fsu's in the two-stage design); but in the two-stage design it is based on variation among both fsu's (stations) and ssu's (grabs within stations). The effect of variation among ssu's was shown above to be insignificant in the analysis even though variation among ssu's was about half as large as variation among fsu's (Table A1), as determined by components of variation calculations from a nested analysis of variance.

Appendix 2

The C.V. differences between optimal allocation and srs result from stratum differences in both means and variances (Cochran 1963, p. 99):

$$V_{\text{srs}} = V_{\text{opt}} + \sum \frac{N_h(S_h - \bar{S})^2}{nN} + \sum \frac{N_h(\bar{Y}_h - \bar{Y})^2}{nN}$$

where V_{srs} is the variance estimator under an srs design and V_{opt} that under a single-stage stratified srs with optimal allocation; N_h is the number of stations in stratum h ($\Sigma N_h = N$); n is the total number of stations sampled (Σn_h; Table 1); S_h is the stratum standard deviation; $\bar{S}$ is a weighted-average standard deviation ($= \Sigma N_h S_h / N$); $\bar{Y}_h$ is the stratum mean; and $\bar{Y}$ is a weighted mean ($= \Sigma N_h \bar{Y}_h / N$). The nature of the C.V. differences between proportional allocation and srs is described similarly to the above equation but with V_{prop} substituted for V_{opt} and the second term on the right-hand side (rhs) omitted (Cochran 1969).

TABLE A2. Mean (top number) and standard deviation (bottom number) estimates, per stratum, for each of polychaetes, crustaceans, and molluscs. Mean and standard deviation contributions are also given; see text for explanation.

	Taxon		
Stratum	Polychaeta	Crustacea	Mollusca
1	2.02	2.02	1.03
	0.33	0.48	0.56
2	2.31	1.97	1.33
	0.67	0.54	0.28
5	2.51	2.05	1.21
	0.52	0.29	0.73
6	1.68	1.38	1.40
	1.18	0.76	1.30
7	1.90	2.03	1.37
	0.79	0.07	0.36
8	2.54	2.00	1.08
	0.21	0.17	0.68
10	2.24	2.00	1.15
	0.33	0.48	0.63
Mean contribution	0.00116	0.00066	0.00030
Standard deviation contribution	0.00145	0.00049	0.00121

It is possible, by using the stratum standard deviation (S_h) and mean ($\bar{Y}_h$) estimates from a single-stage analysis (Table A2), to calculate the relative contributions of differences among standard deviations (term 2 on rhs of above equation) and among means (term 3 rhs) to the differences in C.V. between stratified sampling using optimal allocation and srs (Table 4). The mean and standard deviation contributions are given at the bottom of Table A2. For polychaetes, standard deviation differences contribute more than mean differences; standard deviations larger than $\hat{\bar{S}}$ (= 0.46) occur in strata 2 and 5 while smaller ones occur in strata 1 and 10. (The sample sizes for strata 6, 7, and 8 [2 in each] are too small to provide reliable estimates of stratum standard deviations and hence are given small weights in the above equation.) For crustaceans, mean differences contribute more but the only estimate substantially different from $\hat{\bar{Y}}$ (= 1.96) occurs in stratum 6 (= 1.38). The relatively small N_h in this stratum means that, for crustaceans, real C.V. differences cannot be confirmed between srs and optimal allocation. For molluscs, standard deviation differences contribute much more than mean differences; standard deviations smaller than $\hat{\bar{S}}$ (= 0.64) occur in strata 1 and 2 while a larger one occurs in stratum 5.

Two Electivity Indices for Feeding with Special Reference to Zooplankton Grazing[1]

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VANDERPLOEG, H. A., AND D. SCAVIA. 1979. Two electivity indices for feeding with special reference to zooplankton grazing. J. Fish. Res. Board Can. 36: 362–365.

The electivity indices E_i and E_i' of predator–prey interaction are currently used to quantify particle-size selection by grazers. Under conditions of passive, mechanical particle-size selection predicted by the leaky-sieve model, these indices yield electivity vs. particle-size curves that vary with the shape of the particle-size spectrum of food offered to the zooplankton. In addition to this bias, poor estimates of electivity will be obtained unless only a small fraction of the food is eaten in such experiments. The selectivity coefficient (W_i) used by modelers in feeding constructs and the electivity index E_i^*, derived here, are recommended instead because they do not suffer from the shortcomings described for E_i and E_i'. Moreover, use of W_i's and E_i^*'s is recommended for quantifying selection for many other cases of predator–prey interaction.

Key words: electivity indices, selectivity, selective grazing, predator–prey intraction

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On utilise communément les indices d'électivité E_i et E_i' de l'interaction prédateurs–proies quand il s'agit de quantifier le choix de la grosseur des particules par les brouteurs. Dans les conditions de la sélection mécanique passive de la grosseur des particules prédite par le modèle du tamis, ces indices donnent des courbes électivité vs grosseur des particules qui varient en fonction de la forme du spectre de grosseurs des particules offertes au zooplancton. En plus de ce biais, on obtiendra de pauvres estimations de l'électivité à moins qu'une petite fraction seulement de la nourriture soit mangée au cours de telles expériences. Au lieu de cela, on recommande le coefficient de sélectivité (W_i) utilisé dans la construction de modèles d'alimentation et l'indice d'électivité E_i^*, tel que déduit ici, parce qu'ils n'ont pas les défauts qui ont été décrits pour E_i et E_i'. On recommande en outre d'utiliser W_i et E_i^* pour quantifier la sélection dans plusieurs cas d'interaction prédateurs–proies.

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THE electivity indices E_i and E_i' (Ivlev 1961) have been used to quantify size-selective grazing by zooplankton (Poulet 1973, 1974; Frost 1977). These indices are used to answer the following two questions. First, are particles of certain sizes "selected" in preference to others? Second, does this selection depend on the shape of the particle-size spectrum of food offered? The second question is currently of special interest to zooplankton ecologists. Some work suggests that size selection by copepods is passive and mechanical, a function only of the pore-size distribution of the grazer's filtering sieve and morphology of other mouth parts (Nival and Nival 1973, 1976; Boyd 1976; Frost 1977). Although we recognize the possible importance of mouth parts other than the one or ones with a sieve, this model of size selection will be called the leaky-sieve model, after Boyd (1976). Other work suggests that copepods somehow select peaks of abundance in the particle-size spectrum of food (Poulet 1973; Richman et al. 1977).

In this paper we will show that E_i and E_i' cannot be used to answer the above questions. Boyd (1976) has demonstrated graphically that E_i can vary with the shape of the offered particle-size spectrum. We will support his results analytically and show that the passive size selection predicted by the leaky-sieve model gives values of E_i' that can vary with the shape of the offered particle-size spectrum. Further, we propose the use of two electivity indices that do not suffer from this theoretical shortcoming. A further difficulty with E_i and E_i' is that the experimenter must allow the zooplankton to remove only a small portion of the food offered; otherwise, biased estimates of E_i and E_i' will result. This technical difficulty does not apply to the proposed indices. One proposed index is O'Neill's (1969, 1971) selectivity coefficient (W_i) calculated

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from filtering rates or mortality rates (Vanderploeg and Scavia 1979). The other index is derived here. Although we advocate using the proposed indices for zooplankton, these indices should be useful for other predators as well.

To show that E_i and E_i' vary with the shape of the offered particle-size spectrum under the conditions of the leaky-sieve model, we need the definitions of E_i and E_i' as well as the definition of the filtering rates (F_i) given by the leaky-sieve model:

$$E_i \equiv \left[P_i - \left(X_i \Big/ \sum_i^n X_i\right)\right] \Big/ \left[\left(P_i + \left(X_i \Big/ \sum_i^n X_i\right)\right], \tag{1}$$

$$E_i' \equiv P_i \Big/ \left(X_i \Big/ \sum_i^n X_i\right), \tag{2}$$

and

(3) $F_i \equiv \phi_i \psi$ (Nival and Nival 1973, 1976; Boyd 1976),

where P_i = probability that when feeding occurs the i^{th} kind or size of prey will be selected from all n kinds of prey, X_i = concentration of prey i, ϕ_i = probability that a particle in size category i will be retained by the filtering apparatus and ingested, and ψ = volume of water filtered per unit time by the predator.

Poulet (1973, 1974) and Frost (1977) have approximated P_i by

$$P_i \simeq R_i \Big/ \sum_i^n R_i, \tag{4}$$

where R_i = ration of the i^{th} prey over the time interval of the experiment. Because feeding rate (dR_i/dt) is $F_i X_i$, it follows from equation 3 that $dR_i/dt = \phi_i \psi X_i$. Thus, the relation of R_i to ϕ_i is

$$R_i = \phi_i \int_o^t \psi X_i du, \tag{5}$$

where t = time and u is the dummy variable of integration. Substituting equation 5 for R_i in equation 4 and placing this result for P_i in equation 2, we obtain

$$E_i' = \frac{\phi_i \left(\int_o^t \psi X_i du\right) \left(\sum_i^n X_i \Big/ X_i\right)}{\sum_i^n \phi_i \left(\int_o^t \psi X_i du\right)}. \tag{6}$$

For the special case where all R_i's are small relative to X_i (i.e. for short experiments), X_i in equation 6 may be treated as a constant. In this case,

$$E_i' = \frac{\phi_i \sum_i^n X_i}{\sum_i^n \phi_i X_i}. \tag{7}$$

It is easily seen from equation 7 that E_i' is proportional to ϕ_i but that the value of E_i' can vary with the shape of the offered particle-size spectrum since the quantity $\Sigma X_i / \Sigma \phi_i X_i$ can vary with the shape of the offered particle-size spectrum. The same is true for the general case (equation 6). Equations 6 and 7 predict that although the value of E_i' can vary with the particle-size spectrum offered, the shape of an E_i' vs. particle-size curve will not.

By combining equations 1 and 2, we obtain

$$E_i = (E_i' - 1)/(E_i' + 1). \tag{8}$$

Equations 6 and 8 imply that both the values of E_i and the shape of an E_i vs. particle-size curve can vary with the shape of the offered particle-size spectrum, which has been discussed earlier by Boyd (1976).

We also checked the behavior of the Q and D indices of Jacobs (1974), which were derived from the special case of two kinds of prey. When extended to the case of more than two kinds of prey, Q and D — like E_i' and E_i — vary with the shape of the offered food spectrum.

The selectivity coefficient, W_i, is the weighting factor appearing in the following expression for the probability, P_i, of selection of a given kind of prey (O'Neill 1969, 1971):

$$P_i = W_i X_i \Big/ \sum_i^n W_i X_i. \tag{9}$$

Vanderploeg and Scavia (1979) constrain the definition of W_i by requiring that $\Sigma W_i = 1$. If the W_i's are constants for any set of X_i's, W_i corresponds to the probability that the i^{th} kind of prey will be selected when all kinds of prey are equally abundant (Vanderploeg and Scavia 1979). Chesson (1978) has recently derived a measure of selective predation identical to W_i from a simple stochastic model of prey encounter and capture.

Vanderploeg and Scavia (1979) have shown that W_i is related to filtering rates or mortality rates (m_i) for the n kinds of different prey as follows:

$$W_i = F_i \Big/ \sum_i^n F_i = m_i \Big/ \sum_i^n m_i. \tag{10}$$

Combining equations 3 and 10 yields

$$W_i = \phi_i \Big/ \sum_i^n \phi_i. \tag{11}$$

Since ϕ_i is a fixed property of the filtering animal, equation 11 implies that W_i is independent of the shape of the particle-size spectrum of food available and is only a function of the hole sizes in the filtering apparatus and the animal's ability to handle different sizes of food. If size-selective grazing deviates from that predicted by the leaky-sieve model, W_i for a size category will vary with the shape particle-size spectrum offered. The leaky-sieve model is a specific case of a more general model that may apply to many predator–prey interactions. ϕ_i is the conditional probability (W_i') that if encountered, prey i will be eaten (Vanderploeg and Scavia 1979). ψ corresponds to the volume of space searched per unit time by the predator. W_i''s in other applications may depend on such factors as palatability, prey escape abilities, or defense mechanisms (O'Neill 1969). Thus, W_i is a useful index for pointing out deviations from the leaky-sieve model or deviations in the assumption of constant W_i''s for the more general case.

Vanderploeg and Scavia (1979) showed how to estimate W_i from E_i, E_i', feeding rates, mortality and filtering rates, but recommended using the latter two variables (equation 10) since in that way the experimenter can allow large portions of the available prey to be eaten. The filtering rates are calculated in the usual way:

$$(12) \quad F_i = (V/t)[\ln X_i(0) - \ln X_i(t)] \quad \text{(Gauld 1951)},$$

where V = volume of water available per animal in the experiment and t = length of the experiment. It is possible that if the animals eat a large portion of the available food, F_i will vary with time over the period of the experiment. One might wonder whether time variability in F_i will affect the calculation of W_i. It can be seen that variations in F_i (calculated by equation 12) are due only to changes in ψ (equation 3) for the leaky-sieve model and that W_i is independent of ψ (equation 11). Thus, W_i's can be calculated from F_i's given by equation 12 regardless of whether F_i's are time varying.

In calculating E_i or E_i' from P_i as given by equation 4, zooplankton ecologists must be concerned about the length of the experiment because, as the amount of prey eaten becomes large, equation 4 becomes a poor approximation for P_i. As more food is eaten, concentrations of "desired" (or easily sieved) prey will diminish relative to the less-desired prey. As the less-desired prey increase relative to other prey, the probability of encounter and capture of less-desired prey will be increased, with the end result that estimated values E_i and E_i' for less-desired prey will be biased upwards. Thus, in addition to its theoretical advantage (i.e. constant for the leaky-sieve model), W_i can be more accurately computed since the experimenter can allow the zooplankton to graze down a substantial fraction of the particle-size spectrum.

W_i is defined between 0 and 1. E_i, the electivity coefficient most often used, is defined between -1 and $+1$, with neutral electivity indicated by zero. Since ecologists are used to working with E_i, we derive an index that has the desirable properties of W_i and ranges between -1 and $+1$, with neutral electivity indicated by zero. If equation 1 is examined for the case of equal concentrations of food items, then P_i and $X_i/\Sigma X_i$ are equal to W_i and $1/n$, respectively. Thus, by analogy our new electivity index, E_i^*, is

$$(13) \quad E_i^* = [W_i - (1/n)]/[W_i + (1/n)].$$

E_i^* is not a function of the food spectrum if the leaky-sieve or constant W_i' model holds, since by combining equations 11 and 13

$$(14) \quad E_i^* = \left[\phi_i \Big/ \sum_i^n \phi_i - (1/n)\right] \Big/ \left[\phi_i \Big/ \sum_i^n \phi_i + (1/n)\right].$$

As was recommended above, W_i (appearing in equation 13) should be estimated from equation 10. Further, E_i^*, like W_i, is not affected by the length of time the experiment is run.

The practical significance of the advantages of E_i^* over E_i can be demonstrated by calculating values of E_i and E_i^* from results of hypothetical experiments done with a zooplankter having an assumed ϕ_i distribution. The final food spectra $[X_i(t)]$ were generated from assumed initial spectra $[X_i(0)]$ using the relation

$$X_i(t) = X_i(0)e^{-(\phi_i\psi/V)t}$$

(from equations 3 and 12), the assumed values of ϕ_i, and various values for $(\psi/V)t$. From the initial and final spectra, values of E_i were calculated with equation 4. Values of E_i^*, which are independent of the shape of the offered food spectrum or duration of the experiment, were calculated directly from the values of ϕ_i (equation 14). The assumed ϕ_i distribution was estimated from filtering rates (F_i) determined in a typical grazing experiment with *Diaptomus sicilis*, a freshwater calanoid copepod. Equation 3 was used to calculate ϕ_i, where ψ was assumed to be equal to the largest F_i measured in the experiment. Four different initial food spectra, including a spectrum having the same shape as the ϕ_i distribution, were considered in our analyses (Fig. 1). The effect of the duration of an experiment on E_i, determined for a uniform initial distribution of food is shown in Fig. 2. From the basic definitions of W_i, E_i, and E_i^*, one would expect E_i to approach E_i^* for the case of a uniform distribution of food when the fraction of the available food that is eaten is small. As greater proportions of food are eaten, the departure of the E_i curve from the E_i^* curve gets larger and, as predicted above, values of E_i

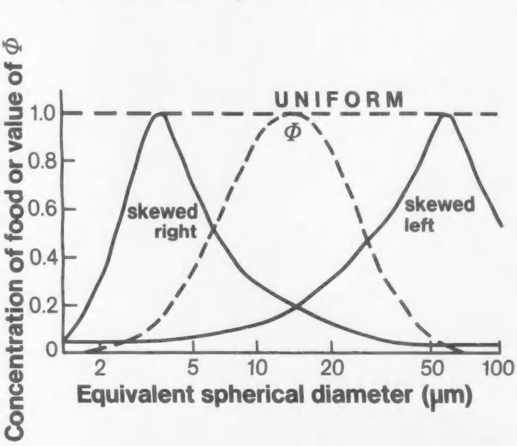

FIG. 1. ϕ distribution and particle size spectra for initial food concentrations.

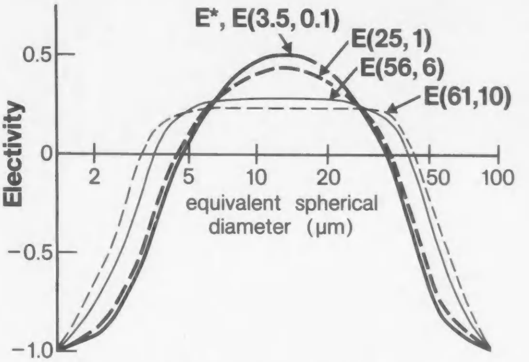

FIG. 2. Curves of electivities vs. particle size as a function of duration of feeding experiment for a uniform offered food spectrum. E^* is the new index and $E(a,b)$ is Ivlev's index with a = percent of food eaten and $b = \psi t/V$ (see text).

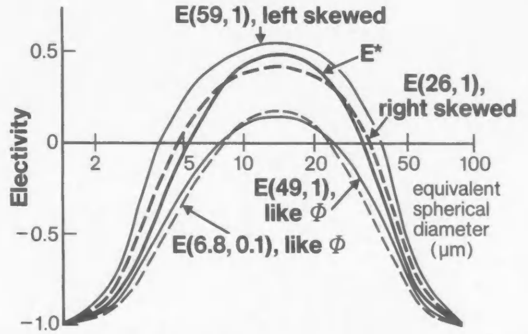

FIG. 3. Curves of electivities vs. particle size as a function of the shape of the offered particle size spectrum. E^* is the new index and $E(a,b)$ are as in Fig. 2.

for small values of ϕ_i (less-desired prey) are biased upwards (Fig. 2).

The shape of the initial food spectrum has a significant effect on the E_i curve (Fig. 3). The E_i curves for the skewed initial distributions of food are considerably different from each other as well as from the E_i^* curve. The E_i curve for the initial distribution shaped like the ϕ_i distribution (Fig. 1) is grossly different from the E_i^* curve and from the E_i curves for the skewed initial distributions. In fact the values of E_i for some size categories even change sign as a function of the initial food spectrum (Fig. 3).

In summary, we recommend the use of the electivity indices W_i and E_i^* to quantify feeding preferences of zooplankton and other animals where W_i''s are expected to be constant. Further, the validity of the assumption of constant ϕ_i's or W_i''s can be tested with these indices. Not only size selection can be investigated with these indices but also preferences based on taste or other factors. Even if the assumption of constant W_i's is only an approximation, one would still expect to get better estimates of selectivity under various conditions of relative prey abundance from W_i and E_i^* than from their analogues, E_i' and E_i.

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Temperature Selection and Estimated Thermal Acclimation by Rainbow Trout (*Salmo gairdneri*) in a Thermal Plume

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Spigarelli, S. A., and M. M. Thommes. 1979. Temperature selection and estimated thermal acclimation by rainbow trout (*Salmo gairdneri*) in a thermal plume. J. Fish. Res. Board Can. 36: 366–376.

Body temperatures of rainbow trout (*Salmo gairdneri*) caught from a thermal discharge into Lake Michigan were used to determine selected temperatures and to estimate acclimation temperatures of this species under field conditions. Approximately 65–75% of the variability in body temperatures was related to water temperature (direct) and fish weight (inverse). Body temperatures increased with increases in discharge temperature, but the difference between body and ambient water temperatures decreased at high water temperatures. The modal body temperature of small fish was 19°C, the final preferred temperature predicted for rainbow trout by some lab studies. The modal body temperature of large fish was 15°C. Estimates of acclimation temperatures indicate that the majority of rainbow trout caught in this discharge area were acclimated to plume temperatures. Estimated acclimation temperatures exceeded ambient acclimation by as much as 10°C for individual fish while group means ranged between 2 and 6°C over ambient acclimation.

Key words: temperature selection, acclimation, thermal plume, rainbow trout, Lake Michigan, body temperature, size effect

Spigarelli, S. A., and M. M. Thommes. 1979. Temperature selection and estimated thermal acclimation by rainbow trout (*Salmo gairdneri*) in a thermal plume. J. Fish. Res. Board Can. 36: 366–376.

Nous avons utilisé les températures corporelles de truites arc-enciel (*Salmo gairdneri*) capturées dans un effluent thermique se déversant dans le lac Michigan pour déterminer les températures choisies et pour estimer les températures d'acclimatation de cette espèce dans des conditions naturelles. Environ 65–75% de la variabilité des températures corporelles est en relation directe avec la température de l'eau et en relation inverse avec le poids du poisson. Les températures corporelles augmentent avec une augmentation de température de l'effluent, mais la différence entre les températures corporelles et celles de l'eau ambiante diminue aux températures de l'eau élevées. La température corporelle modale des petits poissons est de 19°C, ce qui, d'après certaines études en laboratoire, est la température préférée finale prédite pour la truite arc-en-ciel. La température corporelle modale des grands poissons est de 15°C. Des estimations des températures d'acclimatation indiquent que la majorité des truites arc-en-ciel capturées dans cet effluent sont acclimatées aux températures de la zone superficielle. Les températures d'acclimatation estimées sont jusqu'à 10°C supérieures à l'acclimatation ambiante pour des poissons individuels, alors que les moyennes de groupe se situent entre 2–6°C au-dessus de l'acclimatation ambiante.

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Rainbow trout (*Salmo gairdneri*) are attracted to thermal discharges into Lake Michigan and reside in heated plumes for variable periods of time (Spigarelli 1975). Information on temperature selection and acclimation of plume-resident fish is crucial to an assessment of the effects of plume residence. However, vast discrepancies exist between the results of various studies of temperature selection by rainbow trout (summarized by Coutant 1977) and the lack of resolution precludes reliable predictions of temperature selection–acclimation in thermal plumes and resultant effects on fish. A previous lack of attention to biotic and abiotic factors (other than acclimation temperature) affecting temperature selection has compounded the problem of predicting temperature exposure of plume-resident fishes. Thus, a common conclusion is that insufficient data have been collected from natural systems where fish distribution is affected by numerous factors besides temperature (Ferguson 1958; Spigarelli et al. 1974). Reports of the relationship between acclimation and selected temperatures for rainbow trout include (1) an "inverse" relationship (Garside and Tait 1958), (2) no relationship (McCauley et al. 1977), and (3) a "direct"

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relationship (Javaid and Anderson 1967; Cherry et al. 1975, 1977). Laboratory determinations of the "final preferred" temperatures of rainbow trout have varied from 11.6°C (McCauley et al. 1977) to ~19°C (Cherry et al. 1977). Limited field data on temperature selection (Horak and Tanner 1964; Spigarelli et al. 1974; Overholtz et al. 1977) indicate a preference range of 16–21°C for rainbow trout in lacustrine habitats.

A common method of estimating temperature selection by fish in nature is to measure internal body temperature immediately after capture (e.g. Bennett 1971; Spigarelli et al. 1974; Neill and Magnuson 1974). Recently, fish body temperature has gained favor as an indicator of temperature selection under laboratory conditions (e.g., Muller and Fry 1976). The obvious advantage in using body temperature rather than temperature of water occupied is that body temperature is an integration of recent thermal experience and varies less than occupied water temperature.

The primary objective of this study was to obtain sufficient measurements of body temperatures of rainbow trout collected from a thermal effluent area to allow a statistical description of the temperature selection behavior of this species under "natural" conditions (i.e. temperature as a proximate factor rather than the ultimate factor). Secondary objectives were (1) to determine the influence of season, water temperature, fish size, condition factor, and time of day on temperature selection; and (2) to estimate acclimation temperatures of rainbow trout residing in thermal effluent areas.

Study Area and Methods

The Point Beach Nuclear Plant, situated on the western shore of Lake Michigan, near Two Rivers, Wisconsin, draws cooling water from a circular rock-lined crib located 533 m offshore. Once-through cooling effluent is returned to Lake Michigan via two discharge flumes extending 46 m offshore. The typical temperature rise (ΔT) in the cooling water is 10.5°C and discharge velocities at the ends of the flumes range between 0.33 and 0.93 m/s.

Sport fishing censuses were conducted at this site on a daily basis (0600–2100 h) during the periods August–October 1972 and April–October 1973 (Spigarelli and Thommes 1976). Immediately after a rainbow trout was caught from the near-field discharge area, creel census personnel inserted a thermistor through the anus into the intestine of the fish to measure its internal body temperature (T_b) to the nearest 0.1 deg C. Measurements of internal body temperature were completed within 35 s after fish were landed. Date and time of day, fish weight and total length, and intake (T_i) and discharge (T_d) temperatures were recorded for each fish caught during the census. Measurements of body temperature were made on 754 rainbow trout.

Fish body temperatures were grouped by month and season (spring = April, May, June; summer = July, August; fall = September, October) and by weight-class (0–1 kg; 1–2.5 kg; >2.5 kg). Stepwise multiple regressions were performed using seven independent variables: T_i; T_d; weight; length; K-factor ($K = (\text{wt(g)} \times 10^5/\text{length(cm)}^3)$, date, and time of day. A set of convenience variables were created from the data set to characterize the extent of equilibration to discharge temperature and to estimate acclimation temperatures of fish caught from the discharge area:

1. Equilibration Index, $\text{EI} = (T_b - T_i)/(T_d - T_i) = \Delta T_b/\Delta T_d$. This variable is normalized for changes in water temperature and plant ΔT over time and expresses fish responses on a scale of 0–1. A value of 0 represents a body temperature equal to T_i; a value of 1 represents a body temperature equal to T_d.

2. Ambient Acclimation Temperature, $T_{ac^3} = \Sigma T_i/n$, where T_i equals an intake temperature measurement and n equals the number of measurements made over a consecutive 3-d period before the capture of each fish. This factor provides an estimate of the acclimation temperature of a fish residing in ambient temperature inshore waters in the vicinity of Point Beach.

3. Predicted Selected Temperature, T_{s^3}. The selected temperatures of fish acclimated to ambient temperatures (T_{ac^3}) were predicted using the selected-acclimation regression equation given by Cherry et al. (1975) for rainbow trout. T_{ac^3} values were used as acclimation temperatures to calculate predicted selected temperatures.

4. Predicted Avoidance Temperatures, T_{av^3}. The upper avoidance temperature of rainbow trout acclimated to ambient temperatures were calculated in the same manner, using the equation given for upper avoidance temperature (Cherry et al. 1975).

5. Plume Acclimation Temperatures, T_{ac}. Acclimation temperatures of plume-resident fish were estimated from the acclimation-selected temperature equation (Cherry et al. 1975) by assuming T_b equals the mean selected temperature (i.e. falls on regression line).

To estimate the percentages of fish that were acclimated to plume temperatures, we grouped all body temperatures into three categories: $T_b \leqq T_{s^3}$, $T_b > T_{s^3}$, and $T_b > T_{av^3}$. Fish with body temperatures that did not exceed predicted selected temperature for ambient acclimation ($T_b \leqq T_{s^3}$) were classified as ambient acclimated. Those with body temperatures that exceeded the predicted value ($T_b > T_{s^3}$) were classified as plume-acclimated and, as a group, provided an upper limit estimate of the percentage of fish acclimated to elevated temperatures. The group with body temperatures that exceeded predicted avoidance temperatures ($T_b > T_{av^3}$) were considered to be plume-acclimated and provided a lower limit estimate of the number (percent) of fish acclimated to plume temperatures. The group with $T_b > T_{s^3}$ includes fish with $T_b > T_{av^3}$.

A number of assumptions were involved in data manipulation and calculations based on body temperatures:

1. Observed body temperatures were not adjusted for slight changes that could have occurred during the time of capture. Considering the short time required to land a fish (generally <3 min) and the established time response of change in body temperature (Spigarelli et al. 1977) we elected to use body temperatures as measured.

2. Ambient acclimation temperatures (T_{ac^3}) were calculated as the arithmetic mean of hourly intake temperatures measured during the 3 d before a body temperature measurement. If water temperatures were increasing over this 3-d period delayed acclimation (incomplete in 3 d) would result in overestimation of T_{ac^3} while rapid acclimation to rising temperatures would yield underestimates of T_{ac^3}. The reverse would be true for decreasing temperatures. Although the rates of acclimation in fishes, specifically thermal preference acclimation, are not well defined, Javaid (1972)

suggests that rainbow trout acclimate to increased temperatures in ~2 d while cold acclimation requires ~4 d, as evidenced by temperature preference. Although numerous studies (e.g. Brett 1956; Heath 1963) have suggested that fish tend to be acclimated to the highest temperature under variable temperature conditions (indicated by tolerance or resistance criteria), Reynolds and Thompson (1974) found little difference in temperature selection between fish acclimated to constant and variable temperatures. Based on the cited studies we selected the mean of a 3-d period as a representative ambient acclimation temperature.

3. The acclimation-selection-avoidance relationships given by Cherry et al. (1975) were used to estimate acclimation temperatures of rainbow trout because of the similarity to the relationship in our data. The potential problem of curvilinear responses being approximated by linear fits (Richards et al. 1977) does not appear to be serious here since Cherry et al. (1977) show nearly identical results with linear and curvilinear fits to rainbow trout data.

Results and Discussion

VARIABILITY IN BODY TEMPERATURES

Temperature selection of rainbow trout was strongly influenced by changes in water temperature, but other biotic and abiotic factors contributed to the high variability observed in body temperatures. Although body temperatures tended to increase as water temperatures increased, the difference between T_b and T_i decreased at high water temperatures. The relation of T_b to upper (T_d) and lower (T_i) water temperature limits was quite variable over time but the general pattern (Fig. 1) was for T_b to be nearer T_d during cool periods and nearer T_i during warm periods. Considerable short-term variations in water temperatures were the result of three major upwellings (dates 215–227; 238–256; 262–290), and daily variability (ranges) in body temperatures tended to be highest during and following these periods.

The range in body temperatures over the entire study period (9.2–23.5°C) was intermediate between the ranges of T_i (4–21.8°C) and T_d (10.5–31.1°C); this indicates a tendency of rainbow trout to thermoregulate between T_i and T_d, but not at a constant body temperature. Temporal changes in mean and modal T_b are apparent from the data summary in Table 1. Maximum observed body temperatures occurred in July and August when water temperatures were highest and the mean size of fish caught was lowest. Small rainbow trout (<1 kg) selected a range of 14–19°C while large fish selected a range of 13–15°C over the study period. In general, body temperature elevations (ΔT_b) of small fish were greater than those of large fish, and the maximum ΔT_b's occurred in spring.

Mean and modal T_b values (Table 1) are quite similar in large groups since most of the T_b frequency distributions (Fig. 2) approximate the normal. The distributions in Fig. 2C and E are negatively skewed, possibly as a result of the size and season groupings. Reynolds (1977) discusses other causes of skewness in selected temperature distributions. The frequency distribution of all body temperatures (A) shows two modes: the 15°C mode corresponds to that for fish >1 kg (F and G) and the 19°C mode equals that of smaller fish (E). Each season, the measures of central tendency in T_b are related to the body weights of fish in the sample.

Thermal preferenda experiments showing the classical direct relationship between acclimation and selected temperatures for rainbow trout indicate final preferred temperatures of 19°C (Cherry et al. 1975, 1977; McCauley and Pond 1971) and >20°C (Javaid and Anderson 1967) for small rainbow trout. Horak and Tanner (1964) show a modal preference range of 19–21°C (66–70°F) for 569 small rainbow trout collected over an annual cycle from Horsetooth Reservoir, Colorado. Thus, our results tend to confirm studies

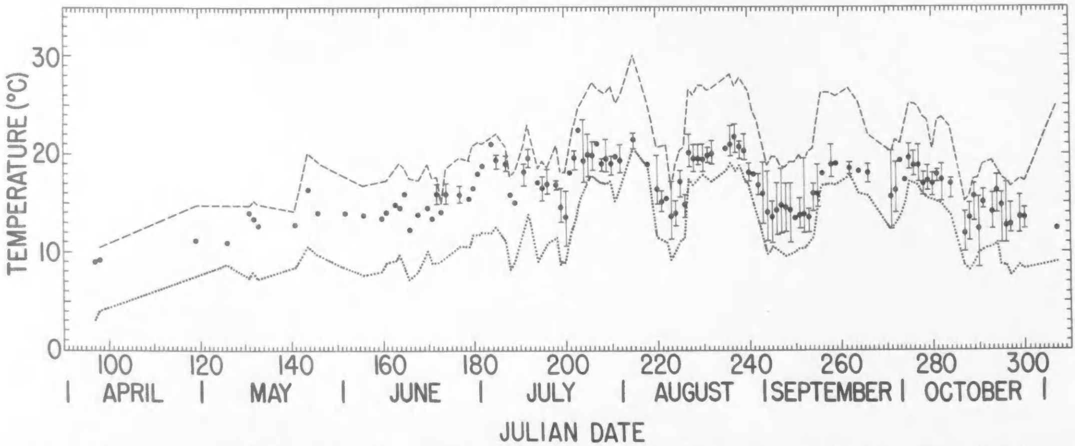

FIG. 1. Daily means (●) and ranges (Φ) of body temperatures of rainbow trout caught during 1973. Mean daily intake (· · ·) and discharge (- - -) temperatures indicate range of available temperatures.

TABLE 1. Summary of body temperatures (°C) and associated variables (means ± SE) for rainbow trout captured in the Point Beach thermal discharge.

Fish group	N	Wt (kg)	T_i	T_d	T_b	Modal T_b	ΔT_b	EI
Total	754	1.72±0.04	12.9±0.1	21.7±0.1	16.5±0.1	15:19	3.6±0.1	0.41±0.01
Small (<1 kg)	278	0.46±0.01	14.2±0.2	23.4±0.2	18.2±0.2	19	3.9±0.1	0.43±0.01
Medium (1—2.5 kg)	175	1.54±0.02	12.5±0.3	21.1±0.3	16.1±0.2	15	3.6±0.1	0.42±0.02
Large (>2.5 kg)	301	2.98±0.04	11.8±0.2	20.4±0.2	15.2±0.1	15	3.3±0.1	0.40±0.01
Spring	35	0.99±0.15	8.9±0.3	17.4±0.4	14.2±0.3	15	5.4±0.2	0.64±0.02
Small	24	0.49±0.05	8.9±0.4	17.8±0.5	14.5±0.4	14	5.6±0.3	0.63±0.03
Medium	5	1.44±0.09	7.9±1.3	15.8±1.4	13.3±1.1	15	5.4±0.2	0.70±0.05
Large	6	2.64±0.10	8.9±0.5	17.2±0.9	13.8±0.5	13	4.9±0.2	0.61±0.05
Summer	282	0.93±0.06	14.8±0.2	24.1±0.2	18.4±0.1	19	3.6±0.1	0.39±0.01
Small	200	0.38±0.01	15.4±0.2	24.7±0.2	19.1±0.1	19	3.7±0.1	0.40±0.02
Medium	35	1.50±0.04	14.3±0.7	23.4±0.7	17.7±0.5	19	3.4±0.3	0.38±0.04
Large	47	2.82±0.11	12.7±0.5	21.8±0.5	15.9±0.4	15	3.2±0.3	0.36±0.03
Fall	437	2.28±0.05	12.0±0.1	20.5±0.1	15.4±0.1	15	3.5±0.1	0.41±0.01
Small	54	0.71±0.03	12.3±0.5	21.2±0.5	16.4±0.3	17	4.1±0.3	0.47±0.03
Medium	135	1.55±0.02	12.3±0.3	20.8±0.3	15.8±0.2	15	3.5±0.2	0.42±0.02
Large	248	3.02±0.04	11.7±0.2	20.1±0.2	15.1±0.1	15	3.3±0.1	0.40±0.01

that show small rainbow trout to have an upper selected temperature of ~19°C.

Indirect estimates of the upper avoidance temperature for rainbow trout can be obtained from Fig. 2 and 3. The frequency distribution of all body temperatures (Fig. 2) shows that only ~3% of the total observations exceeded 21°C. Maximum body temperatures no longer approximated T_d and maximum equilibration indices ceased to approximate unity when discharge temperatures exceeded 20°C (Fig. 3). Strong avoidance was apparent at discharge temperatures exceeding 21°C. Since body temperature does not strictly correspond to water temperature avoidance as measured in experimental gradients and since it is likely that fish can briefly occupy high temperatures without significantly altering body temperatures, we conclude that 23–24°C represents a realistic upper avoidance temperature for small rainbow trout. This estimate is similar to upper avoidance temperatures of 22°C and $\leq$25°C reported by McCauley and Pond (1971) and Cherry et al. (1975), respectively. Large rainbow trout seem to avoid 20–21°C (Fig. 2G).

We observed a general increase in body temperatures as water temperatures increased, but the relative equilibration to discharge temperature (EI factor) tended to decrease as water temperatures increased (Fig. 3). Linear regressions of EI vs. T_d resulted in significant ($P < 0.02$) inverse relationships for each season and relatively high coefficients of determination (0.32–0.51) for groups with large sample sizes. These relationships suggest that natural inshore temperatures in Lake Michigan are usually low relative to the seasonal preferred temperatures (i.e. equilibration indices >0), but occasionally approximate or exceed seasonal physiological optima and preferred temperatures of rainbow trout.

MULTIFACTORIAL ANALYSIS

Multiple regression analyses of body temperature variation in this study (Table 2) shows 3 of 7 tested factors to be consistently related to body temperature: intake or discharge temperature (direct), and fish weight (inverse). Date was highly correlated with T_b in the spring, but not in the other seasons. In addition to the above independent variables, fish length, condition factor, and time of day were tested for linear relationship to T_b. In general, total length did not yield as significant regressions as weight. Condition factor was not significant ($P > 0.05$) except in the fall ($P < 0.0006$; $r^2 = 0.03$) when a slight inverse relationship (slope = −1.58) was observed.

Feeding, general activity patterns, and distribution of fish commonly vary as a function of time of day and a diel pattern could contribute to the unexplained variability in recorded body temperatures. The addition of time of day (hour) to the multiple regression models for total and season groups did not improve the coefficient of determination enough to warrant the retention of hour as an independent variable. However, the analysis suggested that hour of the day was directly related to body temperature during summer and fall; i.e. body temperatures of rainbow trout tended to increase slightly with time between 0600 and 2100. Since there was no diel pattern to T_i or T_d, we hypothesize that diel variability in T_b was related to a diel pattern of orientation by rainbow trout.

On an annual basis, intake or discharge temperatures

TABLE 2. Results of single-factor and two-factor regression analyses of rainbow trout body temperatures and independent factors.

Fish group	T_i	T_d	Wt	Date	Best 2 factor model
Total					$T_b = 9.21 + 0.63\ T_i - 0.51$ wt
r^2	0.72	0.72	0.21	0.04	0.76
Slope	0.69	0.64	−1.07	−0.02	—
P	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
Spring					$T_b = 1.21 + 0.56\ T_d + 0.02$ date
r^2	0.70	0.75	0.10	0.60	0.77
Slope	0.94	0.71	−0.73	0.07	—
P	<0.0001	<0.0001	>0.07	<0.0001	<0.0001
Summer					$T_b = 11.07 + 0.05\ T_i - 0.65$ wt
r^2	0.67	0.67	0.23	0.02	0.73
Slope	0.59	0.57	−1.19	0.02	—
P	<0.0001	<0.0001	<0.0001	>0.01	<0.0001
Fall					$T_b = 8.28 + 0.65\ T_i - 0.27$ wt
r^2	0.64	0.59	0.04	0	0.66
Slope	0.66	0.62	−0.44	−0.58	—
P	<0.0001	<0.0001	<0.0001	>0.2	<0.0001

are equally good predictors of body temperature of rainbow trout residing in this thermal discharge area. Although the spring sample size was small ($n = 35$), discharge temperature appears to be a superior predictive variable in spring, possibly as a result of extended winter residence and plume acclimation by rainbow trout. The slightly higher r^2 for T_i (compared to T_d) in fall could be indicative of the influence of natural temperature cycles and endogenous shifts in selected temperature (Sullivan and Fisher 1953; Neill 1976). The fact that date was highly significant in spring suggests the influence of natural lake warming and the possibility of "anticipatory thermoregulation."

INFLUENCE OF FISH WEIGHT

Although regression analyses showed significant inverse relationships between body temperatures and fish weights in total, summer and fall groups (Table 2), the weight factor was most important in summer, the only season when the weight of fish caught by fishermen was inversely related to water temperature ($P < 0.001$; $r^2 = 0.21$). Thus, high water temperatures in summer apparently favored the residence of small rainbows in the heated plume.

Figure 4A shows the inverse relationship between all body temperatures and fish weights. The parallel relationship between weight of fish caught and water temperature and the extreme short-term variation in water temperatures contributed to the scatter and low r^2 in this regression. To isolate and better describe the influence of weight, we selected "isothermal" periods (consecutive days) when (1) ambient water temperatures did not vary more than ±2°C, and (2) a wide range of fish sizes was sampled. In 10 out of 17 periods, statistically significant ($P < 0.05$) inverse relationships were found between T_b and weight; in the other 7 cases no significance was demonstrated. Three examples of significant relationships are plotted in Fig. 4 (B–D). B and C present data collected during an 8-d period in July, and a 7-d period in August 1973, respectively, which show similar functions. The relationship in D (10 d in September 1973) is less pronounced and is dependent on the four low T_b values for large fish. In general, the analyses of the T_b–weight relationship over time segments showed that the relationship was almost consistently significant from late June through mid-September and tended to be insignificant after late September. Since the strength (r^2) of the relationship was maximum in summer isothermal periods, between the spring and fall spawning times for rainbow trout in Lake Michigan, we hypothesize that the size dependence of temperature selection diminishes during spawning seasons as adults tend to alter normal temperature selection patterns while in search of natal tributaries.

The inverse relationship between T_b and fish weight also could be a function of the body weight effect on rate of heating in fish. Spigarelli et al. (1977) demonstrated a direct (log–log) relationship between rate of change in body temperature and body weight of Lake Michigan fishes; i.e. given equal initial body temperatures and equal exposure times at an elevated temperature, small fish will attain higher body temperatures than large fish. Thus, the apparent relationship between body temperature and fish weight could be totally or partially a function of differences in rates of heating. To test this hypothesis, we corrected body temperatures by (1) assuming initial body temperature to be equal to T_i; (2) calculating the time required to attain measured body temperature assuming each fish entered T_d directly (based on the log–log relationship reported by Spigarelli et al. 1977); (3) assigning equal times to

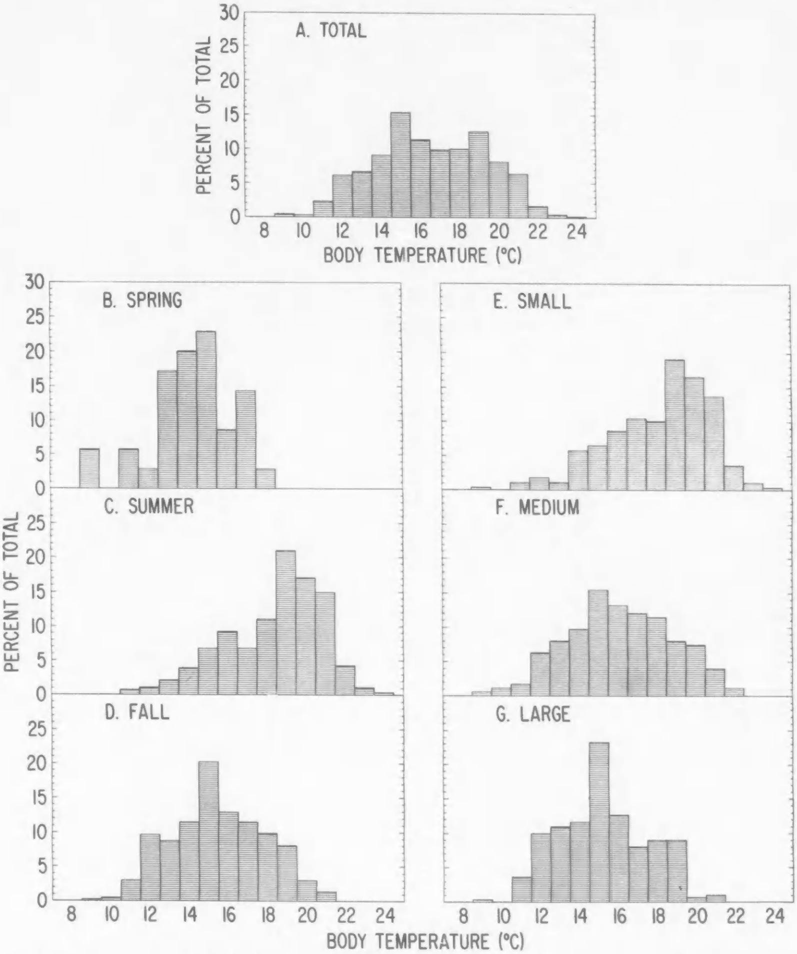

FIG. 2. Frequency distributions of rainbow trout body temperatures grouped by season and weight: spring = April, May, June; summer = July, August; fall = September, October; small ≤1 kg; medium >1 ≤2.5 kg; large >2.5 kg. Body temperatures were rounded to the nearest degree celsius.

all fish (minimum time within the data group); and (4) calculating ΔT_b and corrected body temperature (by subtraction of ΔT_b from measured body temperature).

To determine the influence of body weight on temperature selection (T_b corrected for the heating rate–weight effect) we repeated the regression of T_b on weight. This procedure was performed for two isothermal periods when the uncorrected weight effects (r^2) were greatest (dates 194–201 and 219–227). In both cases, the corrected body temperatures were not significantly related to fish weight. Consequently, we hypothesize that differences in rates of heating between large and small fish could account for differences in measured body temperatures, if all fish are exposed to elevated temperature in a uniform manner. However, the fact that the uncorrected "weight effect" varied from insignificant to very significant between seasons suggests that heating rate is not solely responsible for the size effect on T_b. Our present interpretation is that small rainbow trout have higher upper avoidance temperatures and that size-related differences in temperature selection are diminished in spring and fall when spawning runs result in extended residence in thermal discharges by adult fish.

McCauley and Read (1973) and Barans and Tubb (1973) reported size-related differences in the temperature selection of yellow perch (*Perca flavescens*). Indications of size effects on temperature selection of

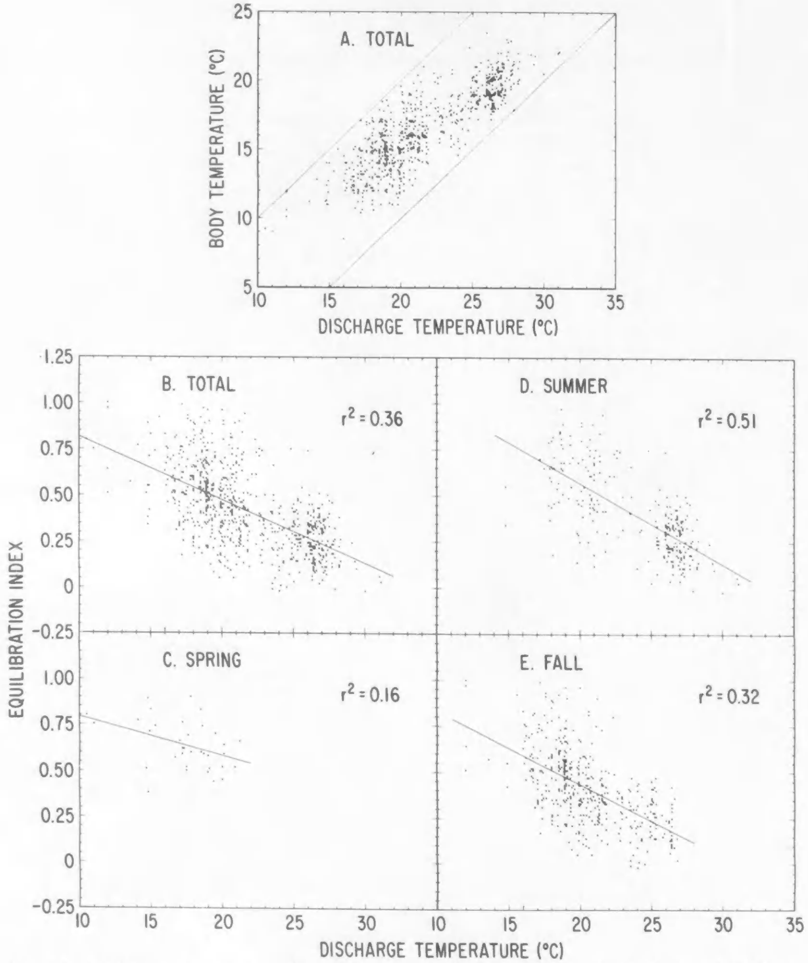

FIG. 3. Body temperatures and equilibration indices plotted as a function of discharge water temperatures. Parallel lines in A represent approximate intake and discharge temperatures ($\Delta T \cong 10°C$).

centrarchids were observed by Neill and Magnuson (1974) while Beitinger and Magnuson (1975) found no significant size effect in bluegill (*Lepomis macrochirus*). A size effect was postulated to be the cause of large differences between results of lab studies of temperature selection by rainbow trout (Javaid and Anderson 1967; McCauley and Pond 1971).

ESTIMATED ACCLIMATION TEMPERATURES

The majority of sampled rainbow trout had body temperatures that exceeded the selected temperatures (T_{s3}) predicted for ambient temperature acclimation (T_{ac3}). In some groups (spring-large; summer-small; summer; small) ≥90% of the body temperatures exceeded those predicted for ambient acclimation (Table 3). The percentages of fish acclimated to plume temperatures (where $T_b > T_{s3}$) decreased with fish size (small > medium > large), but this trend may be the artificial result of our using the available selected–acclimation relationship for small fish (Cherry et al. 1975) to calculate selected temperatures for larger fish.

In Fig. 5 observed body temperatures are plotted as a function of calculated T_{ac3} values. For the purpose of comparison, regression lines are included for predicted values of selected and upper avoidance temperatures of small rainbow trout (Cherry et al. 1975). The difference in elevation of our selected temperature (T_b) lines compared to the predicted indicate significant departures from ambient acclimation for small fish, but

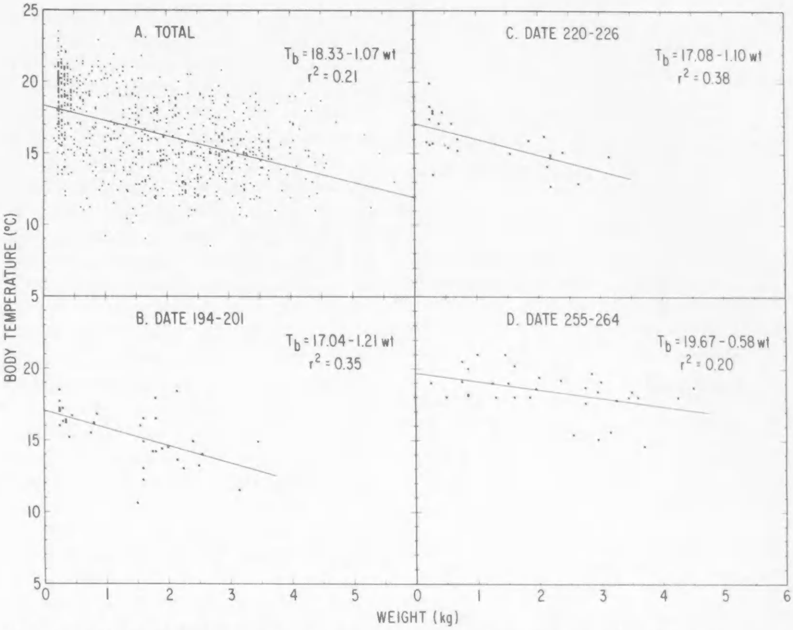

FIG. 4. Relationships between body temperatures and fish weights for all rainbow trout (A) and for fish caught during "isothermal" periods (B–D).

TABLE 3. Estimated percentages of rainbow trout that were acclimated to plume temperatures, mean and excess acclimation temperatures (°C ± SE).

Fish group	N	$T_b \leq T_{s3}$			$T_b > T_{s3}$			$T_b > T_{av3}$		
		n (%N)	T_{ac}	ΔT_{ac}	n (%N)	T_{ac}	ΔT_{ac}	n (%N)	T_{ac}	ΔT_{ac3}
Total	754	179 (24)	9.5±0.2	−1.8±0.1	575 (76)	16.6±0.2	3.2±0.1	211 (28)	18.6±0.2	5.6±0.1
Spring	35	5 (14)	4.9±1.1	−0.8±0.2	30 (86)	12.1±0.4	3.0±0.3	13 (37)	14.0±0.6	4.6±0.3
Summer	282	28 (10)	10.7±0.5	−1.8±0.2	254 (90)	19.0±0.2	4.1±0.2	122 (43)	20.0±0.3	6.2±0.2
Fall	437	146 (33)	9.5±0.2	−1.8±0.1	291 (67)	15.0±0.2	2.4±0.1	76 (17)	17.1±0.3	5.0±0.2
Small	278	19 (7)	9.1±0.7	−1.4±0.2	259 (93)	18.4±0.2	4.3±0.1	141 (51)	19.3±0.3	6.0±0.2
Spring	24	4 (17)	5.6±1.1	−0.8±0.2	20 (83)	12.8±0.5	3.5±0.4	11 (46)	14.4±0.6	4.8±0.3
Summer	200	3 (1)	11.3±1.4	−1.1±0.1	197 (99)	19.5±0.2	4.5±0.2	108 (54)	20.1±0.3	6.3±0.2
Fall	54	12 (22)	9.8±0.8	−1.7±0.4	42 (78)	16.2±0.6	3.5±0.3	22 (41)	17.7±0.7	5.1±0.2
Medium	175	44 (25)	9.4±0.5	−1.8±0.3	131 (75)	15.9±0.3	2.6±0.2	40 (23)	18.0±0.5	5.1±0.3
Spring	5	1 (20)	2.3	−0.9	4 (80)	11.4±0.7	2.4±0.3	0	—	—
Summer	35	5 (14)	9.6±1.6	−2.4±0.7	30 (86)	18.3±0.7	3.1±0.3	12 (34)	19.5±1.0	5.0±0.3
Fall	135	38 (28)	9.5±0.5	−1.8±0.3	97 (72)	15.4±0.3	2.5±0.2	28 (21)	17.4±0.6	5.1±0.4
Large	301	116 (39)	9.6±0.3	−1.8±0.1	185 (61)	14.6±0.2	2.1±0.1	30 (10)	16.2±0.5	4.7±0.3
Spring	6	0	—	—	6 (100)	10.4±0.8	1.9±0.6	2 (33)	12.0±1.6	3.3±0.2
Summer	47	20 (43)	10.9±0.6	−1.7±0.3	27 (57)	16.3±0.7	2.2±0.3	2 (4)	18.8±0.7	7.2±1.2
Fall	248	96 (39)	9.4±0.3	−1.8±0.2	152 (61)	14.5±0.2	2.1±0.1	26 (10)	16.3±0.5	4.6±0.2

the parallel nature of the predicted and observed lines indicates the functional relationship (Cherry et al. 1975) to be correct. *t* tests of differences in slopes and intercepts between our regression lines and those for predicted values of selected temperature showed a significant difference ($P < 0.05$) in intercepts for small fish (Fig. 5A). The regressions for selected temperatures of medium and large fish are nearly identical to each other and are not significantly different from that predicted for small fish.

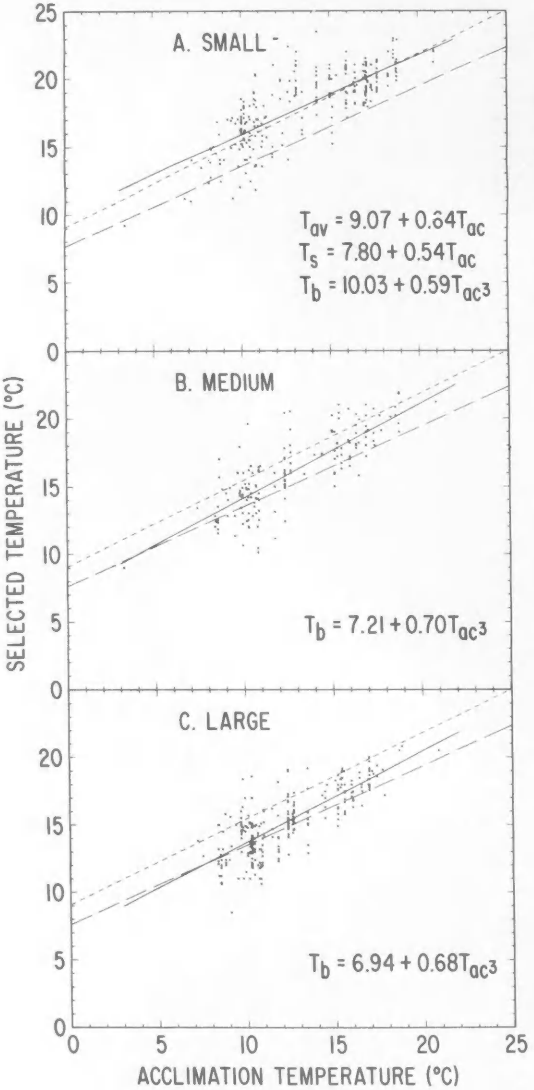

FIG. 5. Relationship of body temperatures (●) to calculated ambient acclimation temperatures (—) for small (A), medium (B), and large (C) rainbow trout. Dashed regression lines represent predicted selected temperatures (— —) and upper avoidance temperatures (- - -) for small rainbow trout (Cherry et al. 1975).

Estimates of mean excess acclimation temperatures (Table 3) range from 2 to 6°C and show a wide range of acclimation states within size and season groups; for example, ~1% of the small fish caught in the summer were classified as ambient acclimated (~11.3°C) while 99% were classified as plume-acclimated (19.5–20.1°C). Conversely, an estimated 43% of the large rainbow trout caught in the summer were acclimated to ambient temperatures (mean = 10.9°C), suggesting limited summer plume residence by large fish or continual exchange of plume and ambient acclimated fish. Mark and recapture studies of fish movements relative to power plant discharges (Romberg et al. 1974b) have shown that rainbow trout (1) are not permanent residents of thermal discharge areas, (2) exhibit strong migratory tendencies, and (3) encounter numerous thermal discharges in their migrations. Thus, at any given time, the rainbow trout feeding in a thermal discharge area form a temporary local population but the individuals differ in their recent acclimation histories. Variability in acclimation within size-groups seems to be a function of season and ambient temperature conditions as well as individual times of residence in a particular plume area.

We theorize that most of the fish with body temperatures in excess of the predicted for ambient acclimation were plume-acclimated, since the attainment of body temperatures greater than predicted would require an ambient-acclimated fish to be exposed to temperatures above selected for 0.5–2 h, depending on fish weight. Also, it is possible that some of the fish with $T_b \leqq T_{s3}$ were plume-acclimated but were caught before they could attain body temperatures exceeding selected for ambient acclimation. Lastly, our data show a statistically significant inverse relationship between selected temperature and fish weight, indicating that the acclimation-selected relationship for small fish would yield underestimates of acclimation temperatures for large fish. Thus, we believe that the upper limit estimates ($T_b > T_{s3}$ in Table 3) of percentages of fish and ΔT_{ac} are most realistic.

SUMMARY AND IMPLICATIONS OF RESULTS

This study provides strong evidence that rainbow trout are attracted to thermal discharges into Lake Michigan and that they increase their body and acclimation temperatures in a predictable fashion. However, ~25% of the variability in body temperatures was not explained by regression and may be related to nonthermal factors such as: rheotactic responses to the discharge; food supply; and thermoenergetic regulation. Assuming body temperatures to be indicative of selected temperatures, small rainbow trout (<1 kg) selected a maximum of 19°C (summer mode), as predicted by some laboratory experiments. Fish larger than 1 kg either selected lower temperatures or did not remain in plumes long enough for their body temperatures to equal those of small fish. Intraspecific size-related differences in temperature selection and acclimation have been noted in other lab and field studies. Randolph and Clemens (1976) observed a segregation of channel catfish (*Ictalurus punctatus*) into size-related groups that fed at discreet times and differed in their thermal acclimation. Beitinger and Magnuson (1975) showed that the presence of social dominants affects temperature selection by subordinate bluegill (*I epomis macrochirus*). Thus, the apparent size-related differences in temperature selection may be a manifestation of heirarchal competition or of intraspecific niche segregation rather than strictly a result of size-related differences in thermal tolerances or requirements.

In general, fish body temperatures were linearly related to discharge water temperatures up to maxima (~23°C) that approximated upper avoidance temperatures for this species. The frequency distributions of body temperatures for season and weight groups were approximately normal and either the mean or the modal temperatures provided good estimates of selected temperature. Body temperature values peaked in summer when water temperatures were highest and when small fish predominated the catch, but the relative equilibration of body temperatures to discharge temperatures was maximum when water temperatures were low (spring > fall > summer). Maximum increases in body temperature over ambient occurred in spring, indicating that (1) some rainbow trout were plume-acclimated before the study (late winter), or (2) rainbows exhibit a strong tendency to acclimate upwards during this period. Frequent short-term fluctuations in natural water temperatures resulted in highly variable body temperatures, indicating the need for studies to compare temperature selection and acclimation rates of fish under constant and variable acclimation conditions.

Our calculations indicate that the majority of rainbow trout caught in this thermal discharge area were acclimated to plume temperatures and that the mean excess acclimation temperatures varied between 2 and 6°C over ambient. The estimated acclimation temperatures are indicative of probable direct effects on plume-resident fish, such as increased food (energy) requirements for maintenance and growth. A few field studies have demonstrated reduced condition or growth in ictalurids (Massengill 1973; Stauffer et al. 1976) and centrarchids (Bennett 1972; Graham 1974; Sappo 1975) that were captured in thermally enriched areas. This effect is commonly attributed to inadequate food supplies and strong thermal attraction. However, Spigarelli and Smith (1976) found no statistical difference between RNA:DNA ratios (indicator of recent growth rates) of thermal plume and reference samples of rainbow trout collected in the fall 1973, i.e. an indication of ample food supply for plume-resident fish. Seasonal high densities of forage fishes near thermal discharges into Lake Michigan (Romberg et al. 1974a) could attract salmonid fishes and may provide energetic advantages to plume-residents. Brett (1971) concluded that sockeye salmon have developed a diel pattern of "thermoregulation" or "energetics regulation" which is an adaptation to the maximization of growth via bioenergetic efficiency (i.e. feeding in high temperature–high prey density areas and then retreating to cool areas to augment food conversion efficiency). Such behavior could reduce the potential for energetic deficits when plume-resident rainbow trout experience seasonal low densities of prey. Conversely, a strong response to preferred temperatures could result in serious energy deficits in plume-resident fishes.

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Method, Validity, and Variability in the Age Determination of Yellowtail Rockfish (*Sebastes flavidus*), Using Otoliths

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A method using otoliths is presented for the age determination of yellowtail rockfish (*Sebastes flavidus*). Most of the details of this method are applicable to other species of rockfish. The method is validated in younger fish by documenting growth of the otolith annular zone by month, and by comparison with ages read from scales. Further validation is provided by length-at-age data, which show monotone growth for both males and females. Age reader variability was analyzed for each age category using random effects analysis of variance. This analysis showed that within-reader variances were similar for the two readers. Although there were significant variance components due to between-reader differences for aging some age categories, the contribution of this variance component to total variability was negligible. The standard deviation for an age determination of an otolith was similar for both readers, ranging from about 0.6 at 8 yr to about 1.6 at 19 yr. For both readers, the coefficient of variation was approximately 0.08 at all ages.

Key words: Sebastes flavidus, age determination, otoliths

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Les auteurs décrivent une méthode de détermination de l'âge de *Sebastes flavidus* à l'aide des otolithes. La méthode est applicable, dans la plupart de ses détails, aux autres espèces de scorpènes. On établit la validité de cette méthode chez de jeunes poissons en démontrant la croissance mensuelle de la zone annulaire de l'otolithe et en comparant avec des âges déterminés à l'aide des écailles. Une autre preuve de validité est fournie par les longueurs à un âge donné, indiquant une croissance similaire des mâles et des femelles. L'analyse de la variance permit de déterminer la variabilité due au « lecteur d'otolithes ». Cette analyse démontre que les variances intralecteur sont les mêmes pour les deux lecteurs. Bien qu'il existe des éléments importants de variance résultant de différences interlecteurs dans la détermination de l'âge de certaines catégories, cet élément de variance contribue de façon négligeable à la variabilité totale. L'écart type d'une lecture d'âge sur un otolithe est semblable pour les deux lecteurs, variant d'environ 0,6 à 8 a et environ 1,6 à 19 a. Pour les deux lecteurs, le coefficient de variation est approximativement 0,08 à tous les âges.

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IN the state of Washington, yellowtail rockfish (*Sebastes flavidus*) are commercially important. From 1972 to 1976, yellowtail rockfish landings averaged 30% of the total rockfish catch, or approximately 2104 t annually. During this period, foreign fleets operating off the coast of Washington also caught substantial quantities of yellowtail rockfish, but these removals have been poorly documented.

Yellowtail rockfish landed in the state of Washington are caught anywhere from the Columbia River (46°N) to Queen Charlotte Sound (52°N), British Columbia. Specimens aged in this study were all taken in 1976, primarily from market samples of catches made throughout this region, the exception being samples from a scientific survey made during September in Queen Charlotte Sound. We shall not consider the precise areas from where samples were taken, since this is unimportant for the current study.

Random sampling was used and, except for the few survey samples, readers were unaware of the length of the fish being aged. In all, 1916 otoliths were interpreted by two readers, providing independent, multiple readings. In this paper, we present details of the method used by readers; give evidence for its validity; and ex-

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amine the statistical variability inherent in the age determination process.

Trout (1954) cites a paper by Reibisch (1899) as being one of the earliest that used otoliths for aging. Since scales were no doubt used earlier, age readers have been using scales and otoliths for over 75 yr. Today it is generally recognized that scales and otoliths are both useful, but usually one is superior for a given species.

When a fish is short-lived and rapid growing, e.g. Pacific salmon, *Oncorhynchus* spp., scales will often prove superior; especially since scales are easier to collect and store than otoliths.

Scales can also be used in the age determination of longer-lived species such as yellowtail rockfish (Phillips 1964). In younger fish, circuli are quite regular and annular rings distinct. However, interpretation of annular rings is more difficult in older fish. Growth becomes slow, and fewer circuli are formed each year. Since annuli are patterns in the circuli, the annuli become extremely difficult to distinguish. In addition, older fish often have a large number of regenerated scales that will obviously not yield proper ages. We have found in the age determination of yellowtail rockfish that scales were reliable only through age 9. Therefore, we have chosen otoliths as our aging structure.

This selection of the otolith is supported by Westrheim (1973) who, in studying Pacific ocean perch (*Sebastes alutus*), found annuli in scales difficult to detect beyond 12 yr. Also, Six and Horton (1977) found that among five structures tested for aging yellowtail rockfish, otoliths provided the most consistent readings.

Method

The method used in reading ages from otoliths is to count the number of hyaline (clear) zones that alternate with the opaque (clouded) zones. It is generally recognized (Holden and Raitt 1974) that an opaque zone is formed during a period of growth (good condition), and a hyaline zone is formed during a period of biological stress (poor condition). Various authors have emphasized a variety of factors influencing zonation. Zonation has been related to temperature and feeding (Molander 1947), temperature and season (Irie 1960), and spawning (Rollefsen 1933; Hickling 1933). In the north Pacific, these factors usually combine to form a winter (hyaline) check. Anyone examining the literature on this subject for the first time would do well to consult Blacker (1974) who describes the apparent inversion of the terms "hyaline" and "opaque" found in some of the literature.

The following procedures for reading ages from rockfish otoliths are used at the Washington Department of Fisheries:

Left otoliths are removed, cleaned, and stored individually in small vials filled with a 30% solution of ethyl alcohol. Before the otolith is stored, it should be freed of the otic sac and other membranes. If an otolith is not properly cleaned, the surface will become chalky and make interpretation difficult. An otolith should be read as soon as possible before deterioration takes place.

For rockfish with large, thick otoliths (e.g. *S. flavidus* and *S. pinniger*), it has been observed that soaking in a 30% glycerine solution will make hyaline zones more visible.

Binocular microscopes with 0.66× objectives and 15× eyepieces were used to view the otoliths. To achieve contrast between hyaline and opaque zones, we submerged the otolith in clear water, concave surface up, in a petri dish with a black velvet cloth background. The purpose of the water is to reduce glare. Reflected lighting combines with the black background to make the hyaline zones appear dark.

Counts are most easily made from the center of an otolith to the outer edge. The areas of an otolith that are easiest to read are species dependent. For yellowtail rockfish, Fig. 1 shows the four best areas in the order of preference: the anterior, the posterio-dorsal, the anterio-dorsal, and the ventral. The shaded areas of this drawing can be used when other areas prove unsatisfactory.

Every otolith should be read from two different areas before an age is assigned. If the same count is made in two different areas, this count becomes the assigned age. When counts from two areas disagree, a third area is read. If two of these three counts agree, the count that agrees becomes the assigned age. If three areas provide three different counts, the reader continues until an agreement is found.

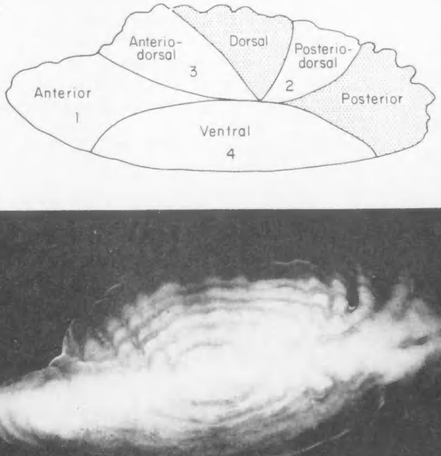

FIG. 1. *Top*, left otolith of a yellowtail rockfish, with regions numbered according to preference for reading; *bottom*, otolith from a 9-yr-old fish.

A major difficulty when trying to achieve agreement is the problem of distinguishing "false checks" from true annuli (Holden and Raitt 1974). False checks are hyaline zones that are not annual rings. The most useful tool for detecting false checks is the width of opaque zones formed annually, which are usually largest in the center, and become narrower toward the outer edge. By recognizing this progression in opaque zone widths, the experienced reader can often detect false checks.

In younger fish, otoliths are thin so that false checks are easily confused with annuli. This problem can sometimes be overcome by turning the otoliths over (convex up), since the convex side is more calcified and false checks less visible.

Older fish present special problems as a reader progresses towards the outer edge where zones may actually have hairline thickness. Yellowtail rockfish otoliths are larger and thicker than those of most rockfish. In older fish, the narrow hyaline zones will sometimes be seen on the side of the otolith. To view these zones, it is necessary to tilt and roll the otolith (not flipping it completely). Under these difficult circumstances, the reader should count from the edge inward and obtain identical counts in three areas before assigning an age.

The procedure we have described constitutes a single aging of an otolith. In our study, the otoliths were aged several times. Final ages, when desired, were calculated by averaging the individual assigned ages and rounding the result. To avoid bias, average ages of the form 1.5 were alternately rounded up and down.

Although these procedures are applicable to most species of rockfish, considerable experience is needed with a particular species before an age reader can apply these criteria confidently and with consistency.

Validity

The method we have described for the age determination of yellowtail rockfish has been validated using three independent methods. First, we have followed the formation of the annular zone showing that one and only one hyaline zone is formed each year. Second, we have compared ages read from scales with ages read from otoliths of the same fish. And finally, we have examined length-at-age data which show that fish aged using the current criteria have monotone growth for both males and females.

EXAMINATION OF THE ANNULAR ZONE FORMATION

Zones formed on otoliths of many young yellowtail rockfish (<12 yr) are quite wide, and it is therefore possible to determine the phase of otolith growth that is taking place at a particular point in time. We refer to the phase of annular growth as the "edge type." Typically, hyaline zones are narrow relative to opaque zones, and the time at which the hyaline zone is formed can conveniently be referred to as a "birthday."

TABLE 1. Numbers of yellowtail rockfish sampled each month having a hyaline edge(H), a narrow opaque edge(H+), or a wide opaque edge (H++).

	Otolith edge type		
Month	H	H+	H++
January		— no samples —	
February	93	0	0
March	70	19	0
April	0	33	0
May		— no samples —	
June	0	49	0
July	0	28	3
August	0	11	23
September	0	0	52
October	0	0	28
November		— no samples —	
December	74	0	64

When a hyaline zone is being formed, the edge is referred to as an "H" edge. If opaque growth is visible beyond the "H" edge, the edge type is referred to as "H+." If a great deal of opaque growth is visible relative to the width of recently formed opaque zones, the edge type is referred to as "H++."

To demonstrate that hyaline zones are indeed annuli, it is necessary to show that one and only one hyaline zone is formed each year. For otoliths with readable edge types, Table 1 shows the sampled numbers of each edge type by month. It is evident that hyaline zones are formed during the period November through March, and only once during the year. For convenience in following year-classes, January 1 is accepted as the "birthday" of all yellowtail rockfish.

These results can be correlated with the maturity stage of fish sampled each month. We shall present data for females only, because the maturity stage for males was difficult to determine. Four maturity categories were used:

Category	Ovary condition
1. immature	small
2. mature	large, yellow, opaque
3. fertilized	large, orange-yellow, translucent; or visible embryos
4. spent, or resting	large, flaccid, red; or moderate size, firm, grey, with some black blotches

The period of reproductive stress would probably occur during the period when eggs become mature, and while embryos were developing. The results from samples in which maturity was examined (Table 2) show these processes occur from possibly September through March. Westrheim (1975) found that March was the principal month of parturition for yellowtail rockfish in the Oregon to British Columbia region. Therefore,

TABLE 2. Numbers of female yellowtail rockfish sampled each month, in each maturity category.

	Maturity category		
Month	Mature	Fertilized	Resting
January	—[a]	—	—
February	4	40	7
March	2	22	10
April	3	0	20
May	—	—	—
June	0	0	60
July	0	0	20
August	0	0	12
September	—	—	—
October	24	11	0
November	—	—	—
December	81	0	0

[a] No samples.

the hyaline zones in adult yellowtail rockfish are possibly spawning checks, because they appear at the time of ovary and embryo development.

COMPARISON WITH AGES READ FROM SCALES

As we have already noted, scales appear to be valid structures for aging yellowtail rockfish through age 9. It seems natural then, to compare ages read from otoliths of young fish with ages read from scales of the same fish.

The table below shows the various scale ages read at each otolith age, for 52 specimens examined in this way.

Otolith age	Scale ages	Percent agreement
1	1, 1, 1, 1, 1, 1, 1, 1	100%
2	2, 2, 2, 2, 2, 3, 3	71%
3	2, 3, 3, 3	75%
4	4, 4, 4, 4, 4, 4, 4, 4, 4, 5, 5, 5	75%
5	4, 4, 5, 5, 5, 5, 5, 5, 5, 5, 6, 6	67%
6	5, 6, 7	33%
7	6, 6, 7, 7, 7	60%
8	none	
9	7	0%

The agreement between scale age and otolith age appears reasonable for this small sample. A matched pairs t-test for statistically testing the difference between scale and otolith ages was unnecessary, because the average of signed differences was zero.

EXAMINATION OF GROWTH

Our method of assigning ages to yellowtail rockfish can be validated against gross errors by examining the growth pattern (fish measured in fork length) of fish we have aged. We would expect the fish to show monotone growth, with the principal length mode increasing with age.

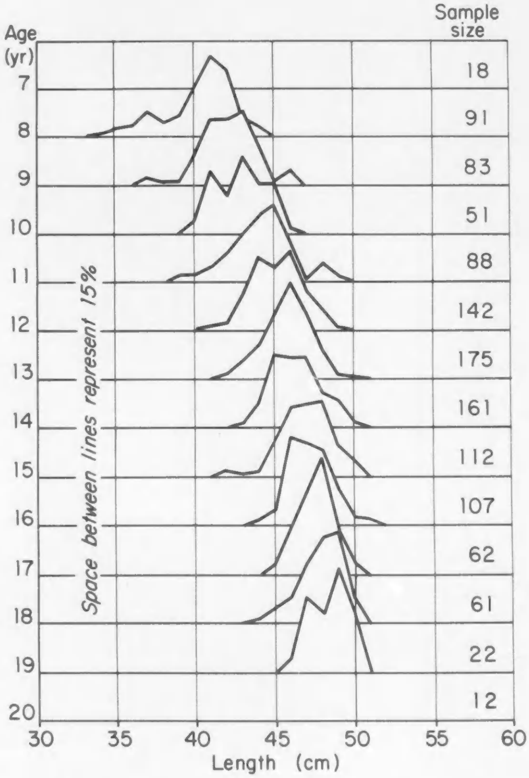

FIG. 2. Length frequencies at each age for male yellowtail rockfish.

Because a preliminary examination of the data indicated there were no obvious differences in growth by area, all of the data were combined. Length frequencies by age (Fig. 2 and 3) show the monotone growth that was expected; however, males and females show a different pattern of growth.

Plots of average length by age (Fig. 4) show that although the growth of males follows the familiar von Bertalanffy growth curve, the growth of females is linear over the range of ages sampled. Six and Horton (1977) found their yellowtail rockfish growth data to be adequately described by the power curve $l_t = at^b$.

Unweighted and weighted fits of growth curves were made using least squares. Unweighted estimates are estimates fitted to the average length at each age. For weighted estimates, the squared deviation of average length is weighted by sample size. These weighted estimates are mathematically equivalent to treating all age-length measurements individually, since it can be shown that both methods lead to the same normal equations. The estimated parameters, along with their standard deviations (shown underneath), are given below:

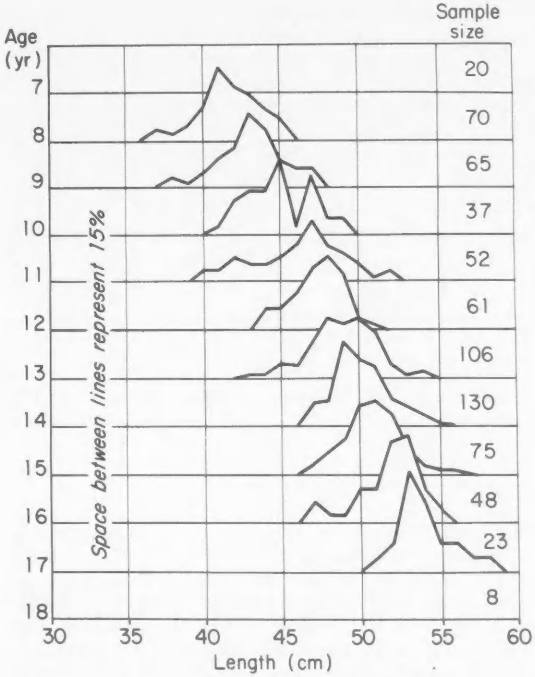

FIG. 3. Length frequencies at each age for female yellowtail rockfish.

males:	unweighted	$l_t = 49.7(1\text{-exp}(-0.172(t+1.71)))$
		(0.362) (0.014) (0.648)
	weighted	$l_t = 49.6(1\text{-exp}(-0.171(t+1.86)))$
		(0.454) (0.017) (0.794)
females:	unweighted	$l_t = 32.6 + 1.21t$
		(0.427) (0.033)
	weighted	$l_t = 32.5 + 1.22t$
		(0.547) (0.043)

Unweighted growth curves for males and females are graphed in Fig. 4.

Variability

To analyze the variability inherent in reading ages from otoliths, 1916 otoliths were given multiple readings. All 1916 otoliths were given a first reading by each of two readers, and 1148 of these were given an independent second reading by the same two readers. From the 1148 otoliths that were given a total of four readings, it was possible to partition the total variance of an age determination into between-reader (σ_A^2) and within-reader (σ_e^2) variance components. To do this, we analyzed the data by random effects analysis of variance. Because variability in age determination increases with age, the data were analyzed by age category.

Let y_{ij} be the jth reading by the ith reader on a single otolith ($i = 1, 2$; $j = 1, 2$). Under the assumptions of

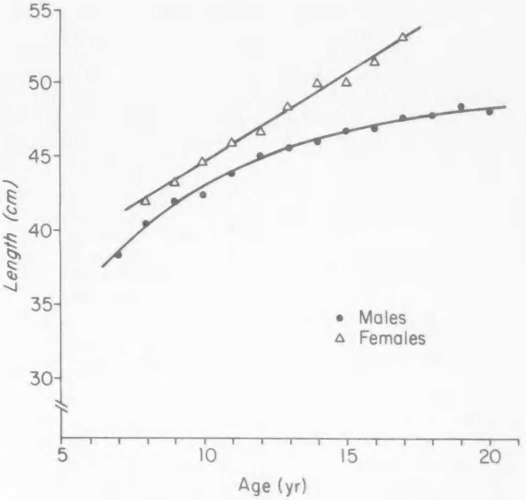

FIG. 4. Average length at each age for male and female yellowtail rockfish, with graphs of growth curves.

the random effects model,

$$y_{ij} = \mu + a_i + e_{ij},$$

where μ = the mean (a fixed effect),
a_i = the component of variability due to choosing reader i (i.e. the between-reader effect).
and e_{ij} = the component of variability due to reader i actually reading the otolith (i.e. the within-reader effect).

It is also assumed that $a_i \sim N(O, \sigma_A^2)$, $e_{ij} \sim N(O, \sigma_{e_i}^2)$ and that all $\{a_i\}$ and $\{e_{ij}\}$ are independent. By assuming observations made on different otoliths are independent, the sum of squares calculated from the above model can be pooled over all otoliths of the same age, providing the analysis of variance shown in Table 3. Readers interested in a more detailed presentation of statistical theory are referred to Scheffe (1959).

As always, the mean squares (MS) are calculated by dividing the sum of squares by the appropriate degrees of freedom. Since MS_{e_1}, MS_{e_2}, and Ms_e are unbiased estimates of $\sigma_{e_1}^2$, $\sigma_{e_2}^2$, and σ_e^2, we shall refer to them as $\hat{\sigma}_{e_1}^2$, $\hat{\sigma}_{e_2}^2$, and $\hat{\sigma}_e^2$.

The hypothesis of equality between within-reader variances was tested for each age category, using the variance ratio $\hat{F} = \hat{\sigma}_{e_1}^2/\hat{\sigma}_{e_2}^2$. Under H_o: $\sigma_{e_1}^2 = \sigma_{e_2}^2$, $\hat{F}$ has a central F-distribution with $\nu_1 = n$ and $\nu_2 = n$ df. Results from this analysis showed there was a significant ($\alpha = 0.05$) difference between within-reader variances for the age 10 category only. This was fortunate because to test the hypothesis H_o: $\sigma_A^2 = 0$, that the between-reader variance component is zero, it is necessary to assume $\sigma_{e_1}^2 = \sigma_{e_2}^2$. Once doing so, the between-reader and pooled within-reader mean squares become inde-

TABLE 3. Analysis of variance table for the random effects model.

Source	Sum of squares	Degrees of freedom	Expected mean squares
Mean	$\frac{\sum(y_{11}+y_{12}+y_{21}+y_{22})^2}{4}$	n	$4\mu^2+2\sigma_A{}^2+\sigma_e{}^2$
Between readers	$\frac{\sum(y_{11}+y_{12}-y_{21}-y_{22})^2}{4}$	n	$2\sigma_A{}^2+\sigma_e{}^2$
Within reader 1	$\frac{\sum(y_{11}-y_{12})^2}{2}$	n	$\sigma_{e_1}{}^2$
Within reader 2	$\frac{\sum(y_{21}-y_{22})^2}{2}$	n	$\sigma_{e_2}{}^2$
Pooled within reader	$\frac{\sum((y_{11}-y_{12})^2+(y_{21}-y_{22})^2)}{2}$	$2n$	$\sigma_e{}^2=(\sigma_{e_1}{}^2+\sigma_{e_2}{}^2)/2$

pendent (Scheffe 1959), and it follows under H_o that $\hat{F} = \mathrm{MS}_A/\hat{\sigma}_e{}^2$ has a central F-distribution with $\nu_1 = n$ and $\nu_2 = 2n$ df.

The null hypotheses $\sigma_{e_1}{}^2 = \sigma_{e_2}{}^2$ and $\sigma_A{}^2 = 0$ together imply there is no difference in the statistical properties of an age determination by the two readers. Examining the expected mean squares (Table 3), we can see that the variance component $\sigma_A{}^2$ can be unbiasedly estimated by

$$\hat{\sigma}_A{}^2 = (\mathrm{MS}_A - \hat{\sigma}_e{}^2)/2$$

Table 4 contains results of the random effects analysis of variance by age category. The P values, $P(F > \hat{F})$, show there were significant ($\alpha = 0.05$) between-reader variance components in the age determination of fish from 12 to 15 yr. However, the values of $\hat{\sigma}_A{}^2/\hat{\sigma}_e{}^2$ indicate that where the estimates of $\sigma_A{}^2$ are positive, $\hat{\sigma}_A{}^2$ averages 11% of $\hat{\sigma}_e{}^2$. Since the variance of y_{ij} is $V(y_{ij}) = \sigma_A{}^2 + \sigma_e{}^2$, the estimated variance of a single reading would be increased only 11% by the addition of $\hat{\sigma}_A{}^2$, a seemingly negligible amount. For this reason, we have ignored $\hat{\sigma}_A{}^2$ in estimating the variance of an age determination.

The estimated variance for an age determination for each reader is given by $\hat{\sigma}_{e_1}{}^2$ and $\hat{\sigma}_{e_2}{}^2$, the within-reader variance estimates. Plots of within-reader standard deviations $\hat{\sigma}_{e_1}$ and $\hat{\sigma}_{e_2}$ by age (Fig. 5), give a good indication of how reader variability increases with age. The standard deviation increases from about 0.6 at 8 yr to about 1.6 at 19 yr and appears linear in between. There is little difference between readers. The corresponding coefficients of variation (Fig. 6) indicate a nearly constant value of approximately 0.08 at all ages. Again, there is little difference between readers.

Concluding Note

Due to problems associated with the deep-water habitat of many rockfishes, it appears their true ages will seldom be known. Thus the absolute bias that exists

TABLE 4. Results of the random effects analysis of variance.

Age (yr)	Number of otoliths (n)	$\hat{\sigma}_e{}^2$	$\hat{\sigma}_A{}^2$	$\hat{\sigma}_A{}^2/\hat{\sigma}_e{}^2$	$\hat{F} = \mathrm{MS}_A/\hat{\sigma}_e{}^2$	$P(F>\hat{F})$
8	50	0.3600	−0.0750	—	0.58	0.9827
9	70	0.5607	−0.1321	—	0.53	0.9982
10	41	0.7805	0.0061	0.0078	1.02	0.4589
11	89	0.7444	0.0168	0.0226	1.05	0.3873
12	129	0.8372	0.1609	0.1922	1.38	0.0154
13	212	0.9104	0.1156	0.1270	1.25	0.0281
14	200	1.0113	0.1137	0.1124	1.22	0.0492
15	119	1.2710	0.2437	0.1917	1.38	0.0190
16	98	1.7143	−0.1378	—	0.84	0.8328
17	53	1.9481	0.0472	0.0242	1.05	0.4085
18	50	2.0500	0.0200	0.0098	1.02	0.4570
19	19	2.6579	0.7763	0.2921	1.58	0.1132
20	14	1.9107	−0.2321	—	0.76	0.6999

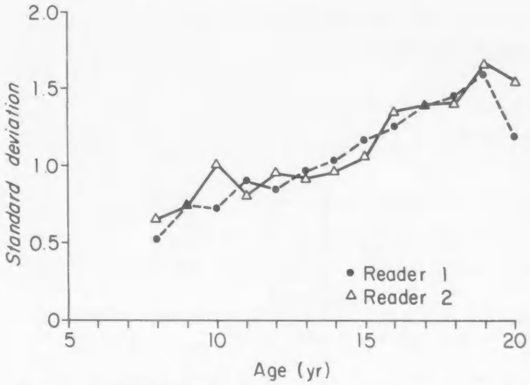

FIG. 5. Standard deviation by age, for reader 1 and reader 2 aging yellowtail rockfish.

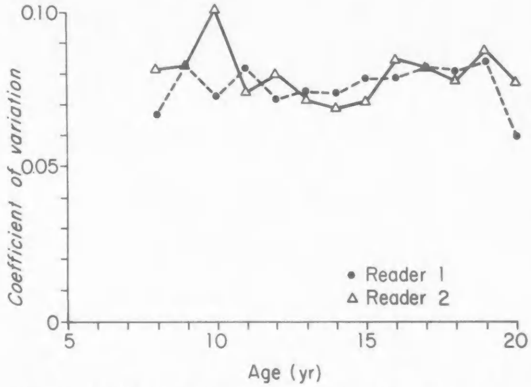

FIG. 6. Coefficient of variation by age, for reader 1 and reader 2 aging yellowtail rockfish.

in their age determination will also be unknown. Relative bias is easy to detect, and we have done so here. It should be noted that relative bias between different agencies is likely to be much more serious. The only way such differences can be corrected is by interagency comparisons of criteria.

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Analysis of the British Columbia Salmon Purse-Seine Fleet: Dynamics of Movement

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HILBORN, R., AND M. LEDBETTER. 1979. Analysis of the British Columbia salmon purse-seine fleet: dynamics of movement. J. Fish. Res. Board Can. 36: 384–391.

Three hypotheses regarding the movement patterns of the British Columbia salmon purse-seine fleet are considered. Two of these hypotheses, that boats move strictly in traditional patterns, or that boats attempt to maximize weekly landed value of catch are rejected. The third hypothesis, that boats move to optimize economic gain, modified by relative desirability of the areas appears to provide a better prediction of patterns. It is shown that when unusually large runs occur in an area, a sufficient number of boats will move into that area to reduce the catch per boat to a level typical of that area.

Key words: boat movement, fleet dynamics, spatial pattern

HILBORN, R., AND M. LEDBETTER. 1979. Analysis of the British Columbia salmon purse-seine fleet: dynamics of movement. J. Fish. Res. Board Can. 36: 384–391.

Les auteurs examinent trois hypothèses relatives aux caractéristiques de mouvements de la flottille de pêche du saumon à la senne coulissante en Colombie-Britannique. Ils éliminent deux de ces hypothèses: que les bateaux se déplacent strictement selon le schéma traditionnel ou que les bateaux essaient de maximiser la valeur au débarquement des prises hebdomadaires. La troisième hypothèse à l'effet que les bateaux se déplacent de façon à optimiser les gains économiques, modifiée par la désirabilité relative des lieux de pêche, semble fournir une meilleure prédiction des caractéristiques des déplacements. On démontre que, quand des remontées exceptionnelles se trouvent dans une région, un nombre suffisant de bateaux se rendront dans cette région pour réduire les prises par bateau au niveau typique de cette région.

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PACIFIC salmon may be the most studied animal resource in the world. They have been under intensive investigation in many countries for nearly a century with thousands of man-years devoted to research and management each year. Yet there exists only a handful of studies of the fleet and fishermen (Crutchfield and Pontecorvo 1969) and none of these can be considered studies of detailed dynamics. In particular, no one has tried to predict the rates of growth of fleets and of catching power and how this will be distributed in space and time. Crutchfield's work stands out as the exception, but his studies and those of his associates have been concerned with large-scale economic models that assume a particular behavior of the fleet; they have not attempted to model the dynamic behavior of the fleet on any but the largest scale. H. Hsu (Department of Fisheries and Oceans, Pacific Region, unpublished data) has described the movement patterns of the B.C. salmon fleet, but has made no attempt to determine what causes these patterns or to predict how they will change with changing fish abundance.

As coastal states artificially enhance stocks, we need a good understanding of the behavior of the fleet in order to analyze the potential impacts of new production. This analysis involves questions concerning fleet development (new boats and gear) and within-season patterns of space–time utilization. There is little point in producing fish that can not be caught, and there is a real danger in producing fish that will stimulate more capitalization and increased fishing pressures on all stocks.

With the above considerations in mind, we have undertaken an analysis of the B.C. salmon fleet. This paper reports on the within-season movement dynamics. We describe the behavior of the fleet and test several hypotheses regarding its movement behavior. We consider only purse-seine vessels in this analysis: they are

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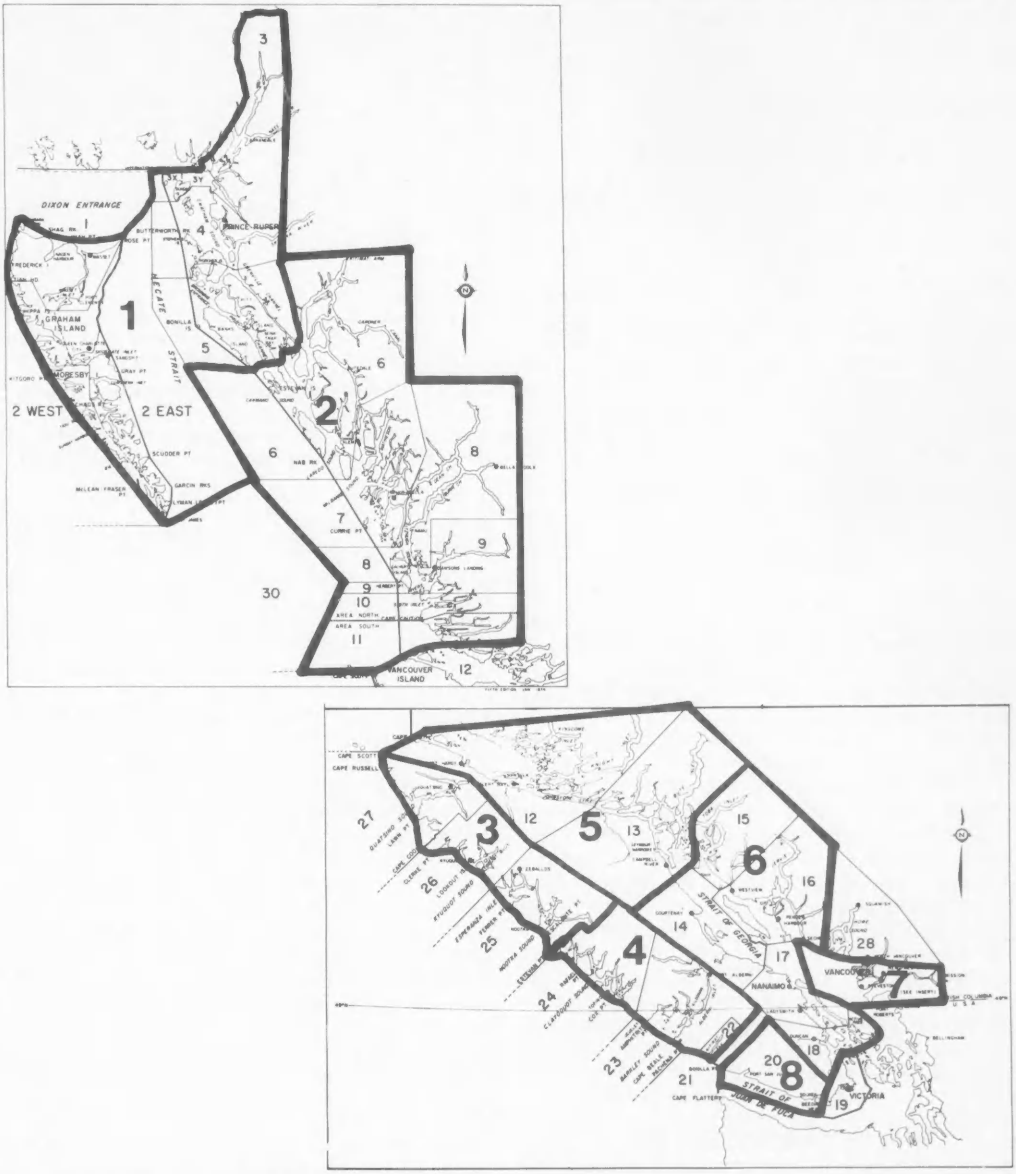
the most mobile segment of the fleet and one that has been growing at the fastest rate. Subsequent papers will deal with questions of catching power and fleet growth.

Data Available

For statistical purposes, the B.C. coastline is divided into 29 areas by the fisheries service. All catches are reported as coming from one of these areas. We have combined these areas into eight larger aggregates (Fig. 1); The seine fleet is highly mobile — most of the boats fish in several areas. The movement patterns of these boats have been described by H. Hsu (unpublished data). Each time a vessel sells fish, a sales slip is filled out: the vessel number, the


DIXON ENTRANCE
GRAHAM ISLAND
MORESBY
2 WEST
2 EAST
HECATE STRAIT
PRINCE RUPERT
BELLA COOLA
VANCOUVER ISLAND
1
2
3
4
5
6
7
8
9
10
11
12
30
AREA NORTH
AREA SOUTH
CAPE SCOTT
CAPE RUSSELL
STRAIT OF GEORGIA
STRAIT OF JUAN DE FUCA
NANAIMO
VANCOUVER
VICTORIA
CAPE FLATTERY
13
14
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16
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FIG. 1. Fishing areas on the British Columbia coast. Small numbers represent the 30 statistical areas. Large numbers represent the eight aggregate areas.

statistical area, the date, the number of pounds and pieces of each salmon species, the price paid, and other pertinent information are recorded. Fish are rarely kept by a seine boat for more than 1 or 2 d, so these sales slips provide an excellent set of data describing the movement patterns and catch success of the individual vessels. Some errors occur in recording; boats may fish in one statistical area for part of a day, fish another area later, and then record all of the fish in the same landing. However, it appears that these data give as good a view of movement and catch as is possible for such a large-scale operation. All of the sales slip records for years 1973–76 were made available to us and these form the basis of this study.

Operation of the Seine Fleet

In each statistical area the seine fleet is regulated by daily openings. Generally, the fishery will open Sunday at 1800 and then run in 24-h or 12-h increments depending upon the intensity of fishing effort and the strength of the salmon run. The fishery is usually open between 2 and 4 d, providing ample time for boats to move between areas between openings but potentially penalizing a boat for moving during an opening. Thus, we regard the basic unit of fishing opportunity as 1 wk. It is our view that fishermen must decide each week where they want to fish during the following week and then allow sufficient time to be in position Sunday afternoon. Seine fishing starts in May and can last through November in some areas.

Patterns of Mobility

We arbitrarily classify seine boats into two classes: stationary boats that fish only in one of our eight aggregate areas and mobile boats that fish in more than one aggregate area. The majority of boats are mobile: in 1973 mobile boats outnumbered stationary boats 5:1 and by 1976 the ratio was 12:1. Obviously the fleet moves and, if we wish to predict effort in a given area, we must understand the determinants of this mobility. Hsu's descriptions suggest that there are groups of fishermen with traditional patterns of behavior and that a large portion of the mobility is due to these patterns, not to changing catch opportunities. This belief is reinforced by interviews with fishermen. They suggest that most of their movement is due to tradition, with some moderation when fishing is better in one area than another. An alternative to this description is one that views the fishermen as economic maximizers: they respond to the catch per effort in different areas. Our first effort was to see if such relationships did exist; could we predict the effort in a given area based on its catch history?

Response of Fishermen to Catch

Fishing performance can be measured in several ways, all of which are variants of catch per unit of effort. Catch can be measured in pieces, weight, or dollar value. Effort can be measured in days fishing, landings, or weeks fishing. We feel that the best measure is landed value per weeks fishing. Certainly a fisherman might prefer to fish only 2 d and land the same value of fish that he might catch in 4 d in another area, but as a basic measure of fishing success, we have used the total dollar value of all fish landed during each week of opening.

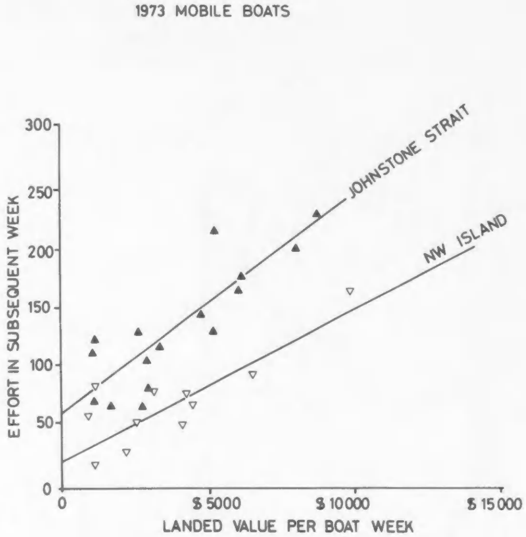

FIG. 2. Number of mobile seine boats operating in two aggregate areas plotted against the landed value per boat week in that area the previous week. Data are for area 2 (NW Vancouver Island) and area 5 (Johnstone Strait) for 1973.

Initially, only the 1973 data were available to us and we examined the relationship between the catch per unit effort (CPE = dollars/week) occurring in an area and the effort observed in the subsequent week. Our hypothesis was that as the CPE improves, more fishing boats will move into that area. The initial results were very promising: Fig. 2 shows the relation between the number of mobile boats fishing in an area (i.e. boat weeks) and the CPE of the previous week. The data are shown for aggregate area 5 (Johnstone Strait) and aggregate 2 (NW Vancouver Island). Both of these areas exhibited very good relationships between CPE and subsequent effort.

The relationships for stationary boats are shown in Fig. 3 for all 4 yr for Johnstone Strait. These are also interesting: apparently only a portion of the boats will fish until the success reaches a certain point (about $1000/wk) and then all the stationary boats in that area will fish. This result suggested to us that there are certain marginal costs, either expenses of fishing or alternative opportunities, that will prevent all boats from operating until certain CPE levels are reached.

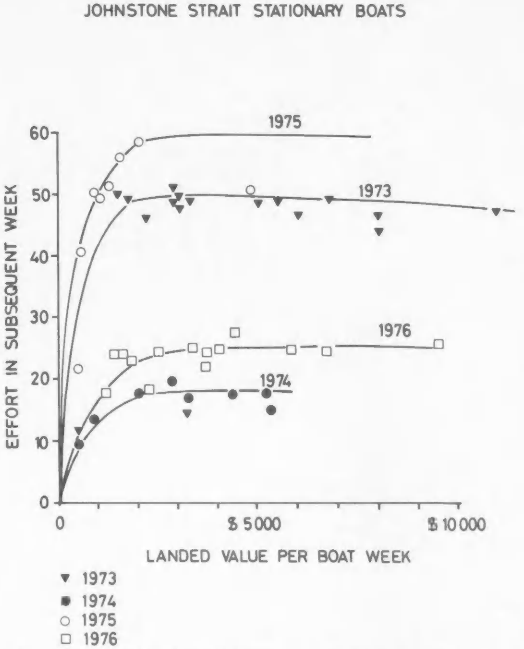

FIG. 3. Number of stationary seine boats operating in Johnstone Strait plotted against the landed value per boat week the previous week. Data are from 1973 to 1976.

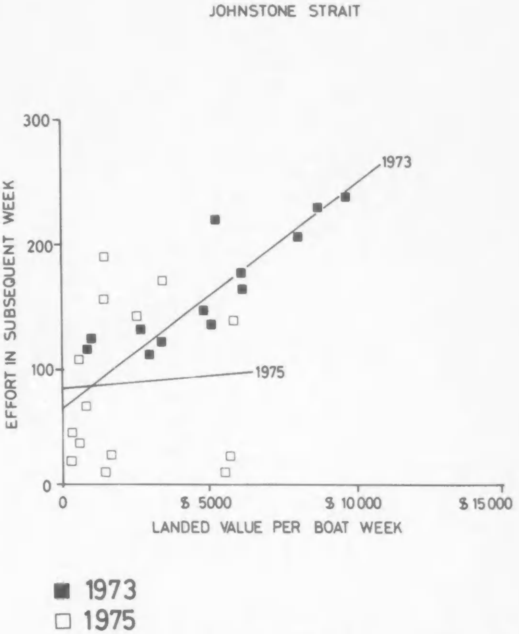

FIG. 4. Number of mobile seine boats operating in Johnstone Strait plotted against the landed value per boat week the previous week for 1973 and 1975. The relationship obvious in 1973 does not occur in 1975.

After initial examination of the 1973 data we felt that some understanding of the fleet pattern was possible. The mobile boats will continue to move into an area as the CPE improves, and the stationary boats operate on a rapidly saturating response curve. Both of these results seemed to indicate some form of economic maximization. However, even before we had access to the 1974–76 data, we began to question the validity of these assumptions. In a good year (as was 1973) a catch of $3000/wk might attract only 100 boats, but in a poor year, $3000/wk might attract every mobile boat in the province. This proves to be the case. Figure 4 illustrates the data for mobile vessels in Johnstone Strait for 1973 and 1975 (1975 was a very poor year). Not only is the slope of the line for 1975 considerably less, but it takes a devout believer to think that the regression line has anything to do with the data. The nice linear relationships we found in 1973 just do not hold up from year to year. They may describe the data well in some instances but they will not aid in predicting the mobility pattern of the fleet.

Similar problems occur with stationary boats. Figure 3 shows that the saturating curve and the threshold seem to be consistent from year to year. However, the level of saturation differs greatly from year to year. This perspective does not provide a particularly useful way of predicting effort.

An alternative to an area by area analysis is to assume a certain behavior on the part of the fishermen and then to make predictions about their behavior on a coast wide basis. If we assume that (1) there is no cost to movement, (2) that all boats are equal, (3) that all areas have equal costs of fishing and are equally desirable as locations to fish, and (4) there is perfect information about fish abundance and regulations in all areas, we might expect that individual boats would move between areas to equalize the CPE in each area. This set of assumptions leads to the prediction that CPE in each area should be about the same; it might go up or down from week to week, but each area should tend towards the provincial average CPE. The efforts should adjust themselves to the CPE. Figure 5 presents the number of boat weeks in each area by week in 1973. This figure shows the timings of the effort and the relative size of the efforts in different areas. More important, it can be seen that the effort in a given area does change over a period of a few weeks, presumably in response to changing abundances of fish. Figure 6 presents the CPE for each area during 1973. It appears from this graph that the areas do not tend towards the same average, but that some areas produce consistently higher CPE than others.

The difference between areas is clear from inspection

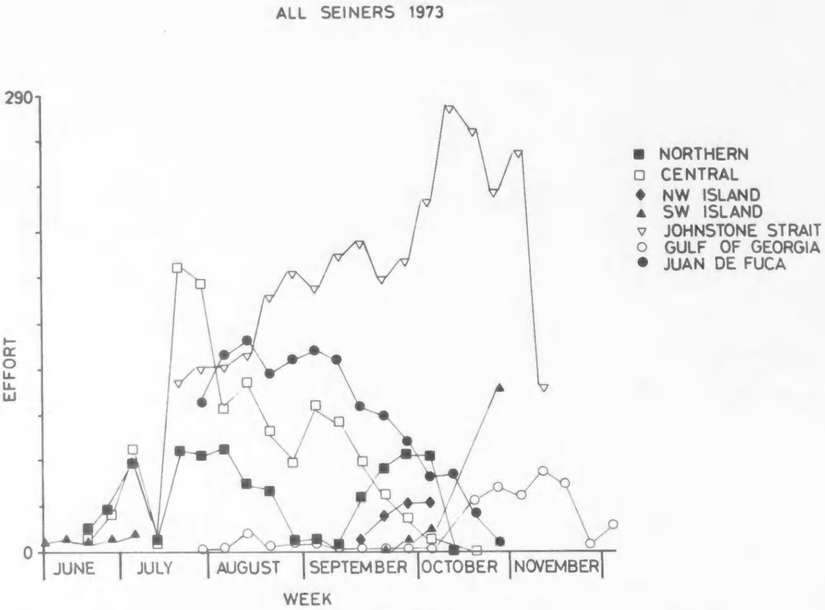

FIG. 5. Number of seine boats operating in each aggregate area each week of the 1973 fishing season.

of Fig. 6 and an analysis of variance shows that there are highly significant differences between areas. Thus we can reject the hypothesis that the mobility is significant enough to average out each area. However, inspection of Fig. 6 does show several useful things: (1) the highest average CPE is found in the Juan de Fuca fishery, one that is exposed to open ocean winds and waves, (2) the lowest CPE is found in the Gulf of Georgia, very protected waters quite close to Vancouver and other amenities, and (3) the other areas fall somewhere in-between. This result suggests that a reason for the higher CPE in Juan de Fuca is that it is a relatively unattractive place to fish: costs are higher because it requires larger boats to fish in the open ocean and the fishing conditions are relatively harsh. Similarly, it suggests that fishermen will accept lower CPE to fish in the Gulf of Georgia because it is a relatively desirable place to fish.

These speculations led us to a new hypothesis that is a variant on the previous "every place is equal." If we modify assumption 3, that all areas have equal costs of fishing and equal desirabilities, and instead assume that areas have different costs of fishing and different desirabilities, then we might expect the boats to move in order to maintain each area's relative CPE. Thus, we would expect that if Juan de Fuca has a relatively poor year, boats will leave that fishery and move to other areas where the CPE is in closer proportion to the costs and desirabilities. The ratio of an area's CPE to the provincial average CPE should remain constant from year to year. Table 1 presents these ratios for each area.

TABLE 1. 1973 value landed per boat week for each area and the ratio to the provincial average. Our hypothesis suggests that these ratios should stay relatively constant from year to year.

Area	Landed value/boat week (CPE) $	% of provincial average
Northern	4072	84
Central	4411	91
NW Vancouver Is.	6081	126
SW Vancouver Is.	5200	108
Johnstone Strait	4453	92
Gulf of Georgia	3234	67
Juan de Fuca	6705	139
Total province	4824	100

Hypotheses About Mobility Behavior

We have thus formulated three hypotheses about the mobility behavior of the seine fleet. These hypotheses are:

I. *Traditional Patterns*: fishermen fish in traditional patterns and the best prediction of efforts for an area will be the historical effort in that area .

II. *Coast Wide Equilization*: fishermen will move from area to area to average out the CPE.

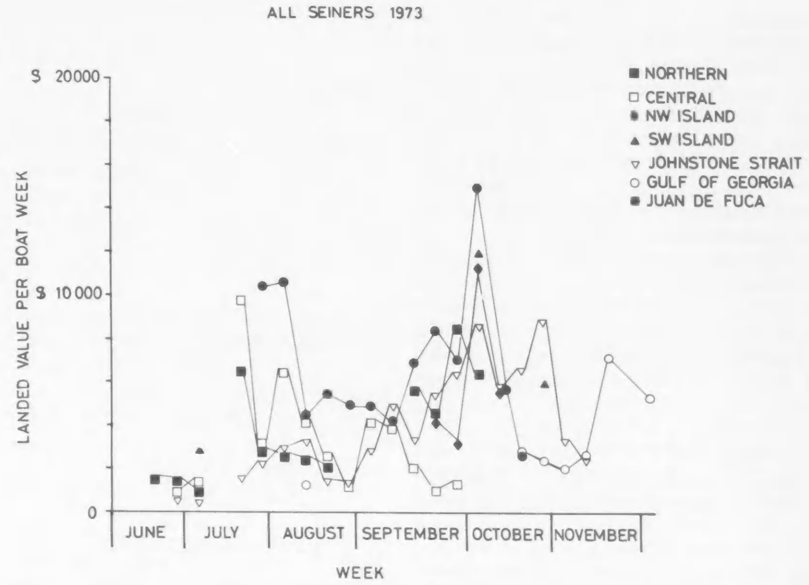

FIG. 6. Landed value per boat week in each aggregate area each week of the 1973 fishing season.

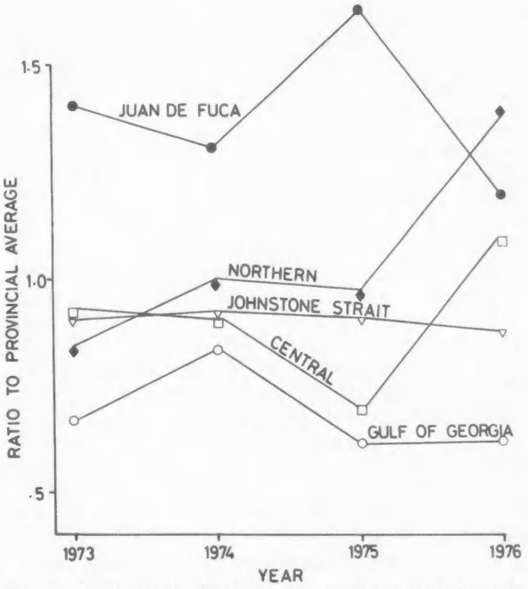

FIG. 7. Ratio of the landed value per boat week in each aggregate area to the provincial average for the major fishing areas.

III. *Area Specific Desirability*: each area has its own unique costs and desirability and fishermen will move between areas maintaining the ratios of the CPE in the different areas.

In the previous discussion we have largely abandoned hypotheses I and II. We will now examine further data to compare the relative merits of the different hypotheses. It is important to note that these hypotheses were formulated before we had access to the 1974–76 data. We had absolutely no idea of what was in those data, so we believe that the analysis does constitute a legitimate "test" of our hypotheses.

Hypothesis III, our working hypothesis, says that the ratio of an area's CPE to the provincial CPE should remain constant. Figure 7 illustrates these ratios for 1973 to 1976; clearly these ratios do remain largely constant over this time span. There is some noise, but there are few changes of rank order among the entire data. Johnstone Strait goes no higher than 92% nor lower than 89%. If we wish to predict the effort in an area, we can use hypothesis III to decide how many boats will have to move from area to area to maintain these percentages. There are a few exceptions — most notable in the northern area. Our hypothesis III does have some flaws. It may be that perfect information is not available to the fishermen: boats may not know of all the other opportunities available to them on a week by week basis. Even more likely is that our assumption about total mobility is not completely true. It does cost money to move from one fishing area to the other and the northern area is at the end of the province, quite distant from the major effort areas of Johnstone Strait and Juan de Fuca. Thus, if the northern area has a good year like 1976, it may not be equalized by boat movement because of the cost of movement. We might expect that areas close to major effort centers will have nearly constant ratios to the provincial average, while areas at the extremes may show more variation. Certainly Johnstone Strait, located in the middle of the province, is the most constant.

To test whether the apparent differences between areas are statistically different, we did the following analysis of variance (ANOVA). If we assume that the value landed per boat week in a given area and in a given year is determined by the provincial average for that year and by the area's long-term average, we can construct a 2-way ANOVA where one effect is the year and the other effect is the area. This test shows that there are very significant ($P > 0.001$) differences between areas and years. Although the 2-way ANOVA model is not identical to the area ratio concept shown in Fig. 7, the ANOVA clearly shows that the areas are different. It is not clear whether the area effect is an additive one or a multiplicitive one, but that is not of major interest.

A strict economic hypothesis that allowed for different operating costs in each area would sugggest that boats should move into areas of "excess" profits until the profit per boat in each area is the same. Unfortunately we have no data on the differences in operating costs between areas and, therefore, we cannot test this hypothesis directly. However, there is no apparent reason for lower operating costs in the Gulf of Georgia than in Johnstone Strait, yet the revenues in the Gulf of Georgia are consistantly lower. Thus we prefer to believe that the differences between areas are due to a combination of economics and relative noneconomic desirability.

A picture has emerged of boat movements that tend to equalize the CPE about a desired level relative to the provincial average with some deviations due to movement costs and distances to other boats. If an area has a poor year, boats will either not come to that area or will leave it, reducing the effort so that the CPE tends towards its desired level. All changes are modified by fishermen's perceptions about current and expected CPE and their feelings about costs, desirability of the different areas, and how long since they saw home port.

An Experimental Test, Barkley Sound

The best test of our hypothesis would be to provide much better or much worse returns to an area and see whether the effort responds to bring the CPE to the desired level. Fortunately, such a natural experiment has been done in Barkley Sound on the southwest coast of Vancouver Island. A lake fertilization experiment was performed in the early 1970s and resulted in relatively large sockeye salmon (*Oncorhynchus nerka*) runs to that area. These runs in turn resulted in increased landed value of fish by seiners (from <\$300 000 to ~\$500 000). Figure 8 shows the total landed value of seine caught fish in statistical area 23 (part of aggregate area 4). It also shows the number of seine boat weeks, the landed value per boat week, and the provincial average landed value per boat week. The total landed value did not increase much from 1973 to 1975. During this period the sockeye runs were increasing, but the chum salmon (*Oncorhynchus keta*) (which constituted half of the landed value in 1973) was nonexistent in 1974 and 1975. The effort increased each year and the CPE decreased. On initial inspection one might have thought that too many fishermen were coming into this area, yet we can see that the provincial average CPE was declining at the same time. Apparently the fleet movement was adjusting the Barkley Sound catch to maintain its position relative to the provincial average.

In 1975 the CPE was very low, much lower than the expected ratio to the provincial average from 1973 and 1974; this may have been due to poor information or high cost of movement to other areas. Figure 8 shows

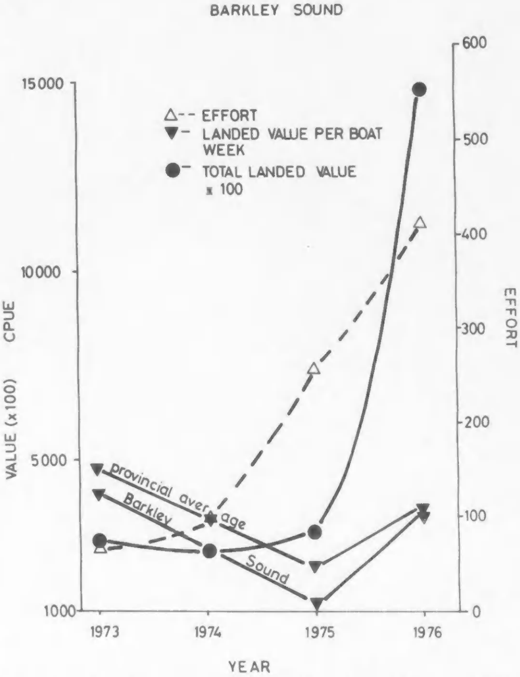

FIG. 8. Development of the Barkley Sound fishery, 1973–76. The total number of boat weeks of effort, the total landed value of all fish, the mean landed value per boat week, and the provincial average landed value per boat week are plotted for 1973–76.

that, on the whole, the mobility of the fleet will ensure that a given area does not get far out of line with its expected ratio to the provincial average.

Discussion

We proposed three hypotheses about the mobility behavior of the salmon seine fleet. We can firmly reject the first two: fishermen do not behave only in traditional patterns and they do not equalize the CPE in all areas. We have provided good evidence that fleet mobility tends to maintain area CPEs relative to the provincial average CPE: high costs and low desirability are characteristics associated with areas above the average, while areas with below average CPEs permit low operating costs and are relatively attractive to fishermen. However, we suggest that costs of movement and imperfect information keep this from being achieved perfectly.

This hypothesis does not require that every boat in the fleet be highly mobile; it only requires that a sufficient proportion of the boats is mobile and that the mobile segment will effectively take advantage of temporarily high catch areas. Because most of the boats fish in more than one area, it is not surprising that there is a sufficient proportion of mobile individuals to provide stabilization.

These results provide a preliminary understanding of the behavior of fishermen. This understanding is crucial for the prediction of the impacts of specific enhancement projects. If the fleet were not mobile, it is possible that new enhancement facilities could produce fish that would not be utilized. Our analysis indicates that this is unlikely. It may be desirable for the management agencies to improve the information system in order to make the fleet behavior even more predictable; the company dispatchers certainly serve a function of this type at present. At the same time managers must be aware of the increases in effort that will accompany any new fish production.

This analysis is only a first step towards understanding the seine fleet dynamics. We now know what determines the space–time movement patterns. Further work is currently under way to determine changes in fleet catching power, factors affecting the building and transfer of new boats into the seine fishery, and the dynamics of movement between the other fisheries and the salmon fishery.

Acknowledgments

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Selective Predation by Drift-Feeding Brown Trout (*Salmo trutta*)

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RINGLER, N. H. 1979. Prey selection by drift-feeding brown trout (*Salmo trutta*). J. Fish. Res. Board Can. 36: 392–403.

Consumption of three species of prey by brown trout (*Salmo trutta*) in a laboratory stream was studied during 7-d experiments. Two drift rates (5 and 10 organisms/min) and three ratios (1:1, 2:1, 5:1) of small:large alternative prey were employed. Responses to prey species stabilized after 4–6 d and 800–1200 prey captures, but no prey was completely excluded from the diet. Size-selective predation was a dominant characteristic of the response. The fish appeared to alter the area (depth) searched in response to prey density; electivity was greatest when prey densities were high. Disproportionate predation on abundant prey ("switching") was a temporary phenomenon, which may have been masked by prey size. Brown trout ultimately achieved 54–91% of a hypothetical diet in which prey are ranked in order of size (energy content). Deviations from an optimal diet may be explained in terms of a feeding strategy that deals with heterogeneous distribution of prey, as well as with the behavioral capabilities of the predator.

Key words: behavior, fish, invertebrate drift, optimal foraging, predation, prey size and abundance, Salmonidae, search image, streams

RINGLER, N. H. 1979. Prey selection by drift-feeding brown trout (*Salmo trutta*). J. Fish. Res. Board Can. 36: 392–403.

Au cours d'expériences de 7 d, nous avons étudié la consommation de trois espèces de proies par des truites brunes (*Salmo trutta*) dans un cours d'eau en laboratoire. Nous avons utilisé deux vitesses de dérive (5 et 10 organismes/min) et trois rapports (1:1, 2:1, 5:1) de petites à grosses proies alternativement. Les réponses aux espèces de proies se stabilisent après 4–6 d et 800–1 200 captures, mais aucune proie n'est complètement exclue du régime. Une caractéristique dominante de la réponse est le choix des proies selon la taille. Les poissons semblent modifier l'aire (profondeur) explorée en réponse à la densité des proies; la sélection est à son maximum quand la densité des proies est élevée. Une prédation disproportionnée sur une proie abondante (« switching ») est un phénomène temporaire qui a pu être masqué par la taille des proies. Les truites brunes réalisent éventuellement de 54 à 91% d'un régime hypothétique dans lequel les proies sont classées par ordre de grosseur (contenu énergétique). Les déviations d'un régime optimal peuvent s'expliquer en fonction d'une stratégie alimentaire tenant compte d'une répartition hétérogène des proies ainsi que du potentiel de comportement du prédateur.

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A voluminous literature on diets in fishes demonstrates the kinds and abundances of food items captured under natural conditions. Many, and perhaps most, fishes forage selectively at least part of the time. Yet the details of the prey selection process are largely unknown, except in a few species that have been studied under simulated lentic conditions (e.g. Beukema 1968; Ivlev 1961; Ware 1971, 1972; Thomas 1977). Available data also provide little understanding of the consequences of prey selection in terms of optimal foraging theory. A notable exception (Werner and Hall 1974) has been the demonstration that predatory behavior of bluegill sunfish (*Lepomis macrochirus*) tends to maximize return with respect to time spent foraging.

Investigations of predation by drift-feeders have lagged behind those of littoral- or pelagic-feeders. This seems surprising in view of a continuing interest in invertebrate "drift" and its role in community stability (e.g. Waters 1972; Allen 1975). Field studies have detected selective predation by stream-dwelling fishes (Reimers 1957; Metz 1974; Griffith 1974), but these do not provide a means of evaluating the pattern of prey selection. Controlled studies of predation by stream-dwelling fishes should broaden our understanding of predation processes in aquatic systems and may prove of value in evaluating perturbations of prey communities in streams.

The objectives of the present study were to describe

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TABLE 1. Mean weight and linear dimensions of prey species.

	Weight (g)	Length (mm)	Width (mm)	Visible surface area (length × width) (mm^2)
Brine shrimp	0.0070	2.69	—	—
Small crickets	0.0127	5.71	1.84	10.51
Small mealworms	0.0128	7.74	1.21	9.37
Large crickets	0.0296	9.30	2.98	27.71
Large mealworms	0.0282	13.48	2.01	27.09

predation by brown trout (*Salmo trutta*) in a laboratory stream; to evaluate the effects of prey size, relative and total abundance, and spatial distribution on the fish's diet during a realistic interval of time; and to determine the extent to which the diet maximizes energy intake. I hypothesized that changes in the diet would be brought about through the formation of a searching image (Tinbergen 1960), the development of a preference for specific kinds of prey (Krebs 1973), and/or by altering the area searched (Beukema 1968; Royama 1970). It was anticipated that the feeding behavior of brown trout might lead to the selection of an optimal diet (MacArthur and Pianka 1966; Schoener 1971).

Materials

Wild brown trout (*Salmo trutta*) were electrofished from Big Creek, a tributary of the North Branch of the AuSable River, Crawford County, Michigan. Individuals were removed from the same 1.2-km stream section at 4- to 7-wk intervals between April 4, 1974 and January 7, 1975. The fish were transported in oxygenated stream water to the laboratory, where they were placed in holding tanks adjusted to the stream temperature. Based on a scale analysis, all but 3 of 50 fish studied were 24–33 mo old; the others were 39–42 mo old. The length and weight of the experimental fish were as follows:

	Mean ± SE (Range)
Total length (mm)	244 ± 11.6 (229–269)
Weight (g)	122.12 ± 21.73 (103.54–162.59)

There were 22 females (3 mature) and 28 males (3 mature).

The prey species were adult brine shrimp (*Artemia salina*), subadult house crickets (*Acheta domestica*), and mealworm larvae (*Tenebrio molitor*). All prey were preserved by freezing but were thawed before use. Samples were drawn from a single large batch of brine shrimp. Crickets and mealworms were sorted to obtain two size categories (Table 1). Samples of each category were dried for 48 h at 65°C, weighed, and burned in a muffle furnace at 600°C. Ash-free dry weights were used to convert wet weight to caloric content, based on published data (Table 2).

Following transport from the stream, the fish were placed in 800-L tanks and acclimated by 1-deg daily increments to 15°C (±1.0°). A 15-h photoperiod, representative of midsummer light conditions, was maintained throughout the study. While in these tanks, the fish were provided 1.25 brine shrimp/L twice daily. The fish began eating brine shrimp within 4–7 d, but detailed observations were not made for a period of at least 3 wk.

A "holding stream" (3.0 × 0.45 × 0.30 m) was used to condition the trout to feeding on drifting brine shrimp. About 15% of the individuals showed little or no feeding response after 3 d and were returned to the holding tanks for a later trial. Fish that fed actively were transferred to an "experimental stream" 2–3 d before an experiment. The stream was an essentially square 1350-L fiberglass trough, 50 cm wide, 12 m in circumference, and filled to a depth of 25 cm (Fig. 1). Continuous circulation of the water was provided by means of an electric pump. The bottom of the stream was covered with gravel 1.5–2.5 cm diam. The straight sections of the tank were provided with windows, and each section was bounded by two 20 × 20-mm mesh screens. One fish was placed in each section; the arrangement of screens prevented visual contact between individuals. A 20 × 35-cm piece of styrofoam suspended above the lower end of each stream section provided overhead cover, and refuge from the current was supplied beneath the cover in the form of a rectangular (10 × 12 × 20 cm) rock. The water surface was smooth, and eddies were eliminated by placement of fine mesh screens above and/or below each section. Mean current velocity, 13.5 cm/s, did not vary significantly among sections. Light intensity was maintained at 18 ± 2 lx incident to the stream surface.

All experiments were run at 17 ± 0.5°C, because feeding

TABLE 2. Estimates of energy equivalents of the prey.

	Joules/g Ash-free dry wt	Source	Best estimate derived from available data	Ash-free dry wt/wet wt[a] mean ± 2 SE (n)	Calculated Joules/g wet wt
Brine shrimp	23218	Von Hentig 1971	22862	0.09159±0.00053 (18)	2093.9
	22510	Calculated from chemical composition of commercial product			
Mealworms	26418	Slobodkin and Richmann 1961			
	27799[b]	Englemann 1961	27816	0.29442±0.00129 (29)	8189.5
	29234	Kitchell and Windell 1970			
Crickets	24669	Cummins and Wuycheck 1971	24669	0.32840±0.00345 (28)	8101.4

[a] No significant differences ($P < 0.05$) were detected in moisture content of small compared to large prey of a given species.

[b] The published value was 6579 calories/g (= 27527 J) dry weight; the figure here is corrected for ash weight.

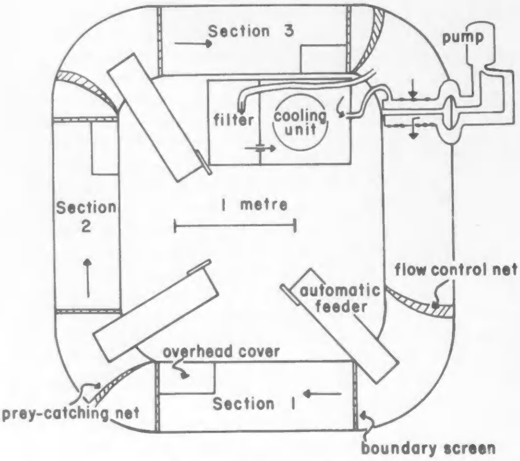

FIG. 1. Diagram of the experimental stream, as seen from above with lighting canopy and covering screen removed. Arrows indicate direction of water circulation.

was most active at this temperature. Water quality was maintained by filtration with activated charcoal and glass wool, and by periodic addition of aged tap water. Dissolved oxygen levels remained near saturation, pH varied between 7.8 and 8.0, and total alkalinity ranged from 46 to 68 mg/L.

Methods

The fish were fed once a day while in the experimental stream; the time of day of feeding varied from 1000 to 1800 h but was always the same (±15 min) for a given individual. Automatic feeders, similar in design to the conveyor belt described by MacPhee (1961), were used to introduce the prey. Crickets and mealworms floated (mealworms were injected with a small quantity of air), whereas brine shrimp were distributed throughout the water column, including the surface. Nylon nets downstream from the fish ensured that each prey item was encountered only once.

The hunger states of the fish were maintained at a similar level by allowing 24 h between trials. Elliott (1972) showed that brown trout evacuated about 95% of the digestible organic matter in a meal of *Tenebrio molitor* in 24 h at 17°C. Examination of the gut contents of four fish fed 25 large mealworms, and four fish fed 50 small crickets, confirmed that Elliott's results were applicable to the present study.

Feeding sequences were recorded by means of a hand-keyed, 20-channel Esterline-Angus events recorder. As each prey item drifted by, I recorded the prey species, and whether the fish approached, attacked, missed, or rejected the item. In certain of the experiments, the vertical distribution of prey and the position of the fish during each attack were recorded with respect to a grid marked on the back wall of the stream channel.

Although some fish rejected prey, this was a rare event. Similarly, approaches not followed by attack were relatively rare, and it was often difficult to distinguish approaches to two items in close proximity. Therefore, the analysis in this paper is based on the number of prey actually eaten.

In the preliminary phase of the study, several drift rates, prey sizes, and exposure times were used to establish realistic conditions for the major experimental phase. The major phase of the study, which employed 27 fish, was carried out from October 14 to February 9, 1975. Following transfer to the experimental stream, the trout were exposed to brine shrimp for 2–3 d before the recording of their behavior ("Day 1"). During Days 2–7 each fish were exposed to one of two drift rates (5/min and 10/min) and three ratios (1:1, 2:1, 5:1) of small:large novel prey. Responses were analyzed during short (5-min) intervals and daily. This design permitted analysis of the role of total and relative prey abundance, as well as prey size, in diet selection. Responses to small crickets:large mealworms vs. small mealworms:large crickets were also examined to evaluate the role of species of prey as opposed to its size. This effect was examined only at the high drift rate. Three fish, randomly assigned with respect to time (date), were used in each treatment.

Results

PREY SELECTION

Brown trout appeared to detect prey visually. Prey were approached from downstream and briefly fixated before being sucked into the mouth. An account of the feeding behavior is given in Ringler (1975).

Differences were evident among individuals in level of feeding activity, as measured by the number of brine shrimp eaten on Day 1. I found no correlation of Day 1 feeding activity with the length, weight, or sex of the fish. At the high drift rate individual variation in timing of the response to novel prey was surprisingly small. Brine shrimp consumption declined abruptly when alternative prey were introduced on Day 2; 5–25 min were required before many novel prey were attacked. The numbers of prey eaten on Days 6–7 were ranked in order of prey size by all three trout, and all maintained some response to brine shrimp throughout the experiment.

Variation in the response attributable to temporal variation in prey availability was removed by calculating the percentage of available prey eaten during each 5-min interval (Fig. 2A). Experiments at the same drift rate but at ratios 2:1 and 5:1 revealed a similar pattern. Except for Day 5 at ratio 5:1, there was little indication that selection of crickets over mealworms increased within a given feeding period. In contrast, the response to brine shrimp generally decreased within each period. These features were also evident from examination of data from individuals and were not an artifact produced by pooling the results from three fish.

When the species combination was changed to large mealworms, small crickets, and brine shrimp, the general pattern was retained (Fig. 2B), although the fish seemed slightly more selective. At the 5:1 ratio the response to large mealworms continued to increase during Days 5 and 6, while that to small crickets decreased. The only major deviation from parallel for

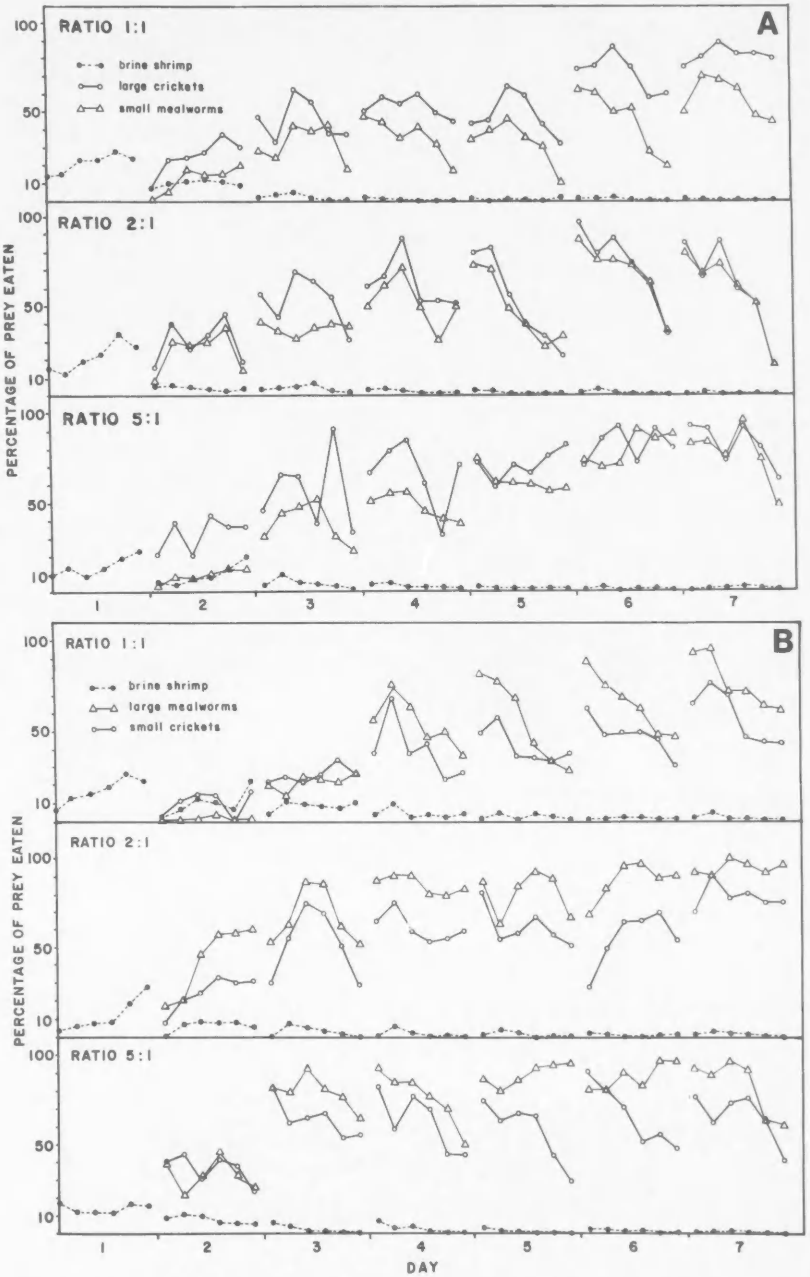

FIG. 2. Mean percentage of prey eaten as a function of time ($n = 3$ fish at each prey ratio of small:large). Drift rate of brine shrimp = 34/min; drift rate of mealworms + crickets = 10/min. Species combinations were (A) brine shrimp, small mealworms, and large crickets; (B) brine shrimp, small crickets and large mealworms.

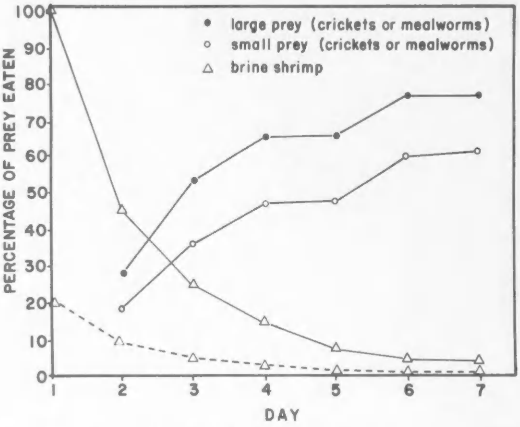

FIG. 3. Comparison of the mean daily response to three prey types. Data are averaged over three prey ratios and two species combinations ($n = 18$ fish). Drift rate of mealworms + crickets = 10/min. Dashed brine shrimp curve was calculated on the basis of 1021 available brine shrimp; solid curve was calculated by assuming an "effective availability" of 200 brine shrimp.

the first series of experiments also occurred at ratio 5:1 (Day 5). These departures from the general pattern evidently were not the result of limitations on prey handling time or stomach capacity, since one would expect that once these began to exert an effect, it would be evident throughout the remainder of the experiment. The pattern on Day 5 also did not suggest development of a search image, since the probability of encounter of large prey was least at ratio 5:1.

At the low drift rate (5 alternative prey/min), individual variation in the feeding response appeared to be more marked than at the high drift rate, particularly at ratio 1:1. One fish, XC-2, never attacked the alternative prey, and another, XB-2, consumed none until Day 4. The rate of encounter, rather than initial differences in the fish, evidently influenced individual variation, since no significant difference was found between experiments in feeding activity on Day 1 (Student's t, 8 df, $= 0.71$; $P > 0.50$).

PREY SELECTION ON PREY SIZE, RELATIVE ABUNDANCE, DRIFT RATE, AND DISTRIBUTION

The experimental design permitted two layouts of the data. Layout 1 tested the effect on the selected diet of (1) the species combination (i.e. small mealworms:large crickets vs. small crickets:large mealworms), (2) the ratio of small:large alternative prey, and (3) time (day). Three-way analysis of variance provided the basis for the following conclusions.

The mean percentage of brine shrimp eaten decreased significantly over time ($F_{5,60} = 30.32$; $P < 0.001$), reaching a minimum by Day 6 (Fig. 3). The shift away from brine shrimp was evidently not affected by any differences in stimuli from different combinations or relative abundances of alternative prey. The daily decrease in brine shrimp consumption was virtually identical for both species combinations. The prey ratio also had no significant effect on the mean response to brine shrimp. The response to crickets and mealworms increased significantly with time and appeared to reach a plateau by Day 6. Differences in response to large mealworms compared to large crickets were not statistically significant. Similarly, comparison of the mean response to small crickets and small mealworms revealed no significant differences between species. Although a few fish seemed to show greater selection for large mealworms, this effect was evidently overridden by that of size and/or abundance.

Prey ratios appeared to affect the response to large prey. Multiple pairwise comparisons (Tukey's T) showed that the mean response at ratio 1:1 was significantly lower than the others ($P < 0.01$). The response to small prey was also lowest at ratio 1:1, although the difference was not statistically significant in the ANOVA model. The biological significance of differences in response among ratios will be considered in a subsequent section.

Of major interest was the comparison of responses among available prey types. The daily response to brine shrimp (Fig. 3, dashed curve) clearly differed from the response to the alternative prey. Because brine shrimp were superabundant (about 20% could be captured), analysis of the percentage eaten exaggerates the difference in response to brine shrimp and alternative prey. This effect was eliminated by assuming that the mean number of brine shrimp eaten on Day 1, when no alternative prey are present, is one estimate of "effective availability." When the response is calculated on this basis (Fig. 3, solid curve) brine shrimp appear to be selected on Day 2, but by Day 3 or 4 the alternative prey receive the greatest response.

The percentage of large alternative prey eaten averaged higher than that of small alternative prey. Considerable variability was evident among individuals in the extent of the difference, particularly early in the experiments when the fish were first exposed to the novel food. A profile analysis (Morrison 1967) indicated that the difference between mean response levels was significant ($F_{1,34} = 11.69$; $P < 0.01$); the profile segments did not diverge significantly from parallel lines ($P > 0.54$). The results of profile analyses for each ratio were substantially the same as those for the lumped data; in each case the percentage of large prey eaten was greater than that of small prey (ratio 1:1, $F_{1,10} = 3.50$; $P < 0.05$, ratio 2:1, $F_{1,10} = 4.52$; $P < 0.05$; ratio 5:1, $F_{1,10} = 10.48$, $P < 0.01$).

Separate analyses for Days 2–4 and 5–7 showed no evidence that the profile segments diverged from parallel lines. Thus, although the trout became increasingly selective of the alternative prey relative to brine

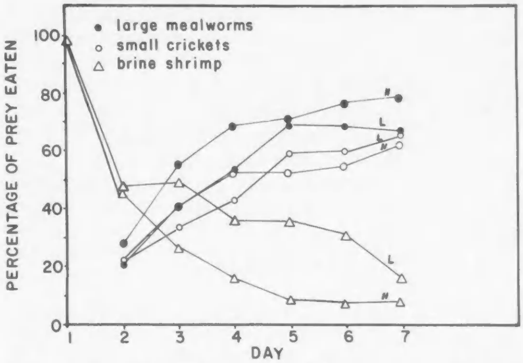

FIG. 4. Comparison of the mean daily response among all prey species. Data are averaged over three prey ratios ($n = 9$ for each drift rate). Brine shrimp curve was calculated by assuming an "effective availability" of 200 brine shrimp. H = high drift rate; L = low drift rate.

shrimp, their response to crickets and mealworms tended to increase together. This suggests that the fish were not forming a searching image for large prey to the gradual or complete exclusion of small, but simply exhibited a preference for large prey. As they became increasingly familiar with the new and larger prey, the number eaten gradually increased at the expense of brine shrimp captures. Some of the fish during Days 6–7 approached but did not attack brine shrimp; such behavior occurred only rarely before experience with alternative prey. This points to an active selection process rather than the "visual filtering" (Tinbergen 1960) characteristic of the formation of a searching image. Whatever its internal basis, the selection process permitted the capture of at least some brine shrimp throughout the experimental period.

Layout 2 tested the effect on the diet of two drift rates of alternative prey (5 and 10/min), as well as the ratio and time effects. A 3-way ANOVA provided the basis for the following interpretation of the results. Brine shrimp consumption decreased significantly ($F_{5,60} = 9.27$; $P < 0.001$) during the experiment at both drift rates of alternative prey (Fig. 4). At the high rate the response to brine shrimp seemed to decline more rapidly and to a lower level than at the low rate, but this effect was not statistically significant ($P > 0.10$).

The percentage of large mealworms eaten increased significantly over time at both drift rates, reaching a plateau by Day 5 or 6. The mean response (61.9%) at the high drift rate was greater than the response (53.2%) at the low drift rate, but the difference was not statistically significant ($P > 0.25$). The mean percentage of small crickets eaten also increased significantly with time; the response averaged over 6 d was virtually identical at both drift rates.

As the ratio of small crickets:large mealworms was increased at the low drift rate from 1:1 to 2:1 to 5:1, consumption of small crickets increased from 24.5 to 54.5 to 61.8%, respectively. The number of alternative prey eaten averaged 42.72, 84.28, and 94.07 at the respective ratios. I found a similar ranking in the response to large mealworms. Evidently the fish did not simply respond to the combined stimulus from the crickets and mealworms. For example, the visible surface area (Table 1) for crickets and mealworms totaled 2820, 2406, and 1991 mm^2 for the respective ratios; the number of alternative prey eaten was ranked in opposite order. Possibly the trout respond initially to the most abundant novel prey, because of the greater probability of encountering them. The response, however, is soon generalized to the preferable large prey, and these are ultimately selected. This conjecture is supported by the finding that on Day 2 at ratio 5:1 (low drift rate) small crickets were selected over large mealworms for the first 20 min. Initial selection of small prey at ratio 5:1 also occurred at the high drift rate (Fig. 2B); this phenomen lasted about 10 min.

When data from each drift rate were treated separately the difference in mean response to crickets and mealworms approached statistical significance at the high drift rate ($F_{1,16} = 3.44$; $P < 0.10$); this was due to the significantly greater ($P < 0.05$) response to mealworms during Days 5–7. Since profiles were parallel ($P > 0.50$), the trout evidently did not increase their response to large mealworms at the expense of small crickets. Use of an electivity index (Ivlev 1961) suggested that the trout were most selective when alternative prey were most abundant (Fig. 5). This pattern agrees qualitatively with the mathematical predictions of Emlen (1966), and the empirical results of Ivlev (1961). A 3-way ANOVA demonstrated that the mean difference in electivity between drift rates was significant for brine shrimp ($F_{1,12} = 11.88$; $P < 0.01$), though not for mealworms ($F_{1,12} = 1.83$; $P > 0.15$).

It appeared that the inflection point in the percentage of prey eaten (Fig. 4) occurred later at the low drift rate for both large and small prey. This result may be explained in terms of a cumulative learning process (Holling 1965): each time a prey item is captured the fish "learns a lesson," which is gradually extinguished in the absence of reinforcement. At the low drift rate the time between encounters provides longer intervals during which extinction can occur, as well as fewer opportunities for learning. The limits to the response (asymptotes) during the later days of the experiments may also have been influenced by the learning process. Consumption of alternative prey species reached an asymptote, for both drift rates, at about the same percentage level (70–75% for large mealworms; 51–57% for small crickets). If limits were related only to physical constraints, e.g. minimum prey handling time or stomach capacity, one would expect the fish to capture similar absolute numbers (not per-

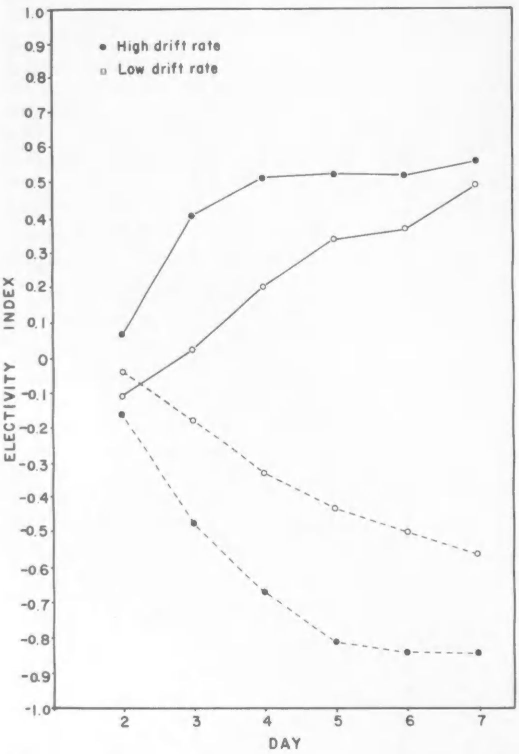

FIG. 5. Comparison of "electivity" (Ivlev 1961) at high and low drift rates ($n = 9$ fish at each drift rate). Solid lines indicate electivity for large mealworms; dashed lines show electivity for brine shrimp.

centages) of prey at the two drift rates.

Response limits were also determined by the time required to approach, attack, and swallow a prey item. Thus, some prey invariably were missed as others were captured. Since prey consumption declined markedly within certain feeding periods (Fig. 2), satiation effects were also evidently involved. One may infer that by Day 4 (high drift rate) or Day 5 (low drift rate) a substantial reduction in hunger level occurred within the feeding period. Contrary to Ivlev's (1961) predictions, the trout did not become increasingly selective as they approached satiation, at least in terms of their response to crickets vs. mealworms.

Unlike the other prey types, brine shrimp were distributed throughout the water column. Analysis of variance showed that significant differences ($F_{4,510} = 321$; $P < 0.01$) existed in brine shrimp availability among the five depths studied. More than 40% of the brine shrimp were found at the surface, and 70% were in the upper half of the water column. A difference in brine shrimp abundance also existed between the first two time intervals ($F_{5,510} = 32.4$; $P < 0.01$), and the increase in available brine shrimp was greatest in the surface layer. This change in availability, however, probably had little influence on the pattern of prey selection previously described. Even during the first 5 min brine shrimp were 2–4 times as abundant as both alternative prey species combined; thereafter, the number of brine shrimp remained nearly constant.

Analysis of the trout's response to brine shrimp on Day 1 showed that the main effects of time ($F_{5,510} = 10.23$; $P < 0.01$) and of depth ($F_{4,510} = 8.13$; $P < 0.01$) accounted for most of the variation in number of brine shrimp eaten. Availability evidently influenced consumption rate. For example, at Depth 5 (19–25 cm) a relatively small but constant number of brine shrimp was eaten, but this represented a large and increasing fraction of those available at this depth. The percentage of brine shrimp eaten was ranked in approximately reverse order of the number available at each depth, a result suggesting that brine shrimp were superabundant.

A more satisfactory measure of changing responses among depths was the fraction of all brine shrimp in the diet captured at each depth. The mean contribution of brine shrimp to the diet varied significantly among depths ($F_{4,510} = 30.33$; $P < 0.01$), but a more important finding was the significant interaction of depth with time ($F_{20,510} = 1.88$; $P < 0.05$). At the surface and at Depths 2 and 3 an increase occurred in the contribution of brine shrimp, whereas in the lower depths (4 and 5) a decrease occurred. These data document a tendency of the fish to move from lower to higher depths; an upstream movement toward the point of prey delivery was also documented (Ringler 1975). These results suggest that within relatively short (30-min) periods brown trout can concentrate their attacks in areas of highest prey density.

The upward movement of the fish continued when alternative prey were introduced on Days 2–7. Data on the vertical distribution of feeding were available from experiments in which brine shrimp and one species of alternative prey were presented on Days 2–7. The number of brine shrimp eaten decreased, but the fraction attributable to surface captures greatly increased. This effect was demonstrated by all five fish presented 150 small crickets for 15 min, along with 500 brine shrimp. The experiment also showed that more than 6 times as many crickets as brine shrimp were attacked at the water surface, where brine shrimp were 1.33 times as abundant as crickets. A difference existed, therefore, in trout responses to prey species, apart from that resulting from different spatial distributions. Differential predation rates appeared to be largely attributable to the size discrepancy among species.

I tested this hypothesis by employing tiny crickets (mean length = 2.4 mm; wt = 0.0043 g) with approximately 80% of the visable surface area of brine shrimp. The crickets were introduced (5/min) with brine shrimp (33/min) during 6-d experiments. The mean

TABLE 3. Estimated energy content per prey item.

	Mean wt (g) ± 2 SE	Estimated Joules/g wet wt (from Table 2)	Joules/ prey item
Brine shrimp	0.0070 ± 0.00000	2093.9	14.64
Small crickets	0.01276 ± 0.00002	8101.4	103.39
Small mealworms	0.01284 ± 0.00003	8189.5	105.14
Large crickets	0.02957 ± 0.00006	8101.4	239.53
Large mealworms	0.02813 ± 0.00005	8189.5	230.37

response of five brown trout to brine shrimp remained nearly constant. Attacks on crickets increased gradually over time, but when the superabundance of brine shrimp was taken into account, predation on brine shrimp (the larger prey) was 2.1 times that on crickets after 6 d.

SELECTIVE PREDATION AND ENERGY CONTENT

The trout in the experimental system fed selectively. As long as 4–6 d and 800–1200 successful attacks were required before responses to prey seemed to stabilize. The abundance and spatial distribution of prey affected the outcome, but prey size appeared to be the overriding factor in the selection. Based on the caloric differences among prey species (Table 3), size selective predation should lead to increased energy intake. I calculated, for an observed daily ration, the energy content of a diet obtained by feeding at random (prey consumption in proportion to abundance in the drift). The energy content of an optimal diet was also calculated, where the largest prey is taken first; if the total number of captures exceeds the number of large prey, the fish takes the next largest item, and so on. This method assumes that the time taken to attack and eat different species was identical. Because the total number of prey eaten was very similar during Day 1 (brine shrimp only) and Days 2–7 (brine shrimp, crickets, and mealworms), this assumption appears valid here.

Comparison of the observed energy intake with the "random" and "optimal" values provided one measure of the consequences of selective predation (Fig. 6). Variation in random and optimum values resulted from changes in the number of prey eaten, and to a small extent from daily fluctuation in mean prey weight. Initially, the observed energy gain differed little from that predicted by random feeding. By Day 7, however, selective predation had more than tripled average energy intake relative to a random diet. The "optimum" was approached but never reached, the peak response averaging 87% of optimum by the end of the experiment.

Considering the prey ratios separately, there was no mean difference between observed and random on Day 2 for ratio 1:1. In fact, in some individuals the energy content of the diet on Day 2 was considerably below the random value. These instances correspond to a continued consumption of large numbers of brine shrimp. A positive departure from random almost always occurred by Day 3, however, and all of the trout tended to increase their energy intake toward the hypothetical optimum value.

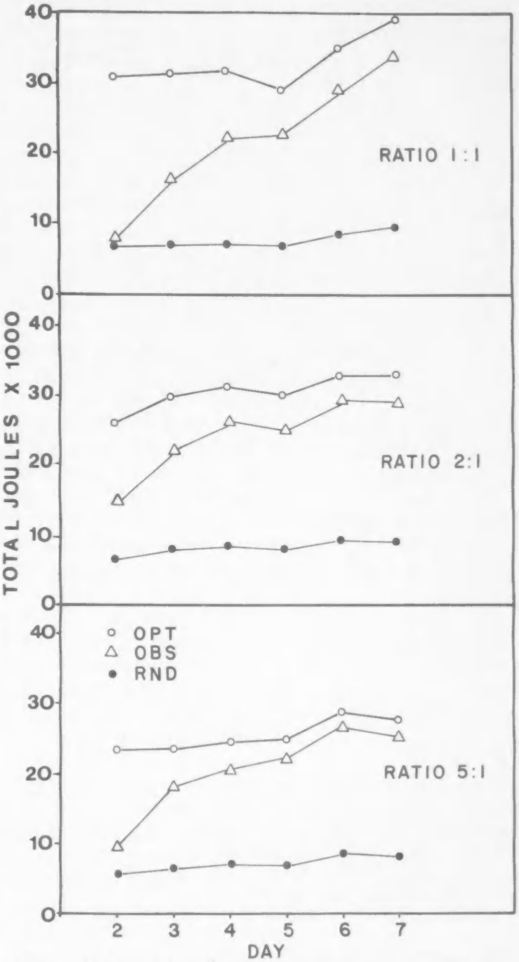

FIG. 6. Daily changes in the mean energy content of a hypothetical optimum diet (OPT) based on a ranking of prey in order of size, the observed diet (OBS), and a random diet (RND) obtained by feeding on prey in proportion to their abundance in the drift. Mealworms + crickets = 10/min; brine shrimp = 34/min. Data are averaged over both species combinations (n = 6 fish for each ratio).

Comparisons among ratios, as well as other analyses can be made by expressing the data in the form of an "optimization index": OI = Observed Energy Intake/

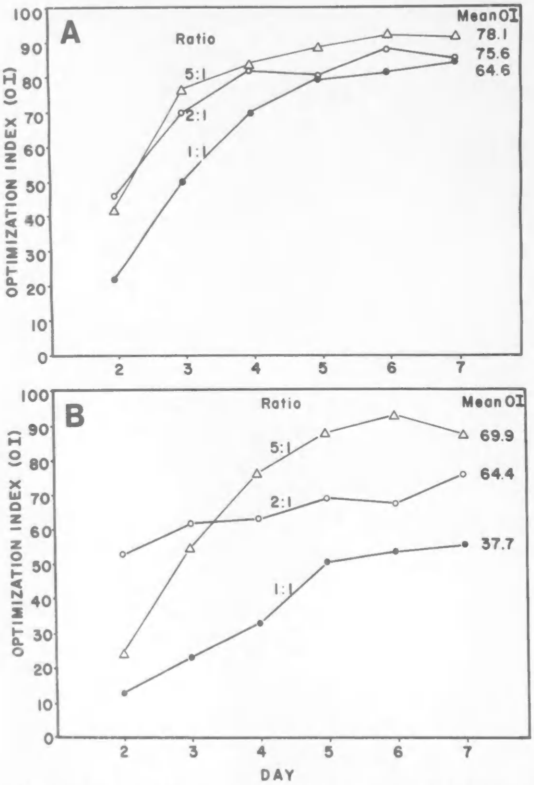

FIG. 7. Comparison among prey ratios of the daily optimization index. Data are averaged over both species combinations (n = 6 fish for each ratio). A, High drift rate (brine shrimp = 34/min; mealworms + crickets = 10/min); B, low drift rate (brine shrimp = 34/min; mealworms + crickets = 5/min).

Optimum Energy Intake × 100. The peak value ranged from 54.30 to 91.20, depending on drift rate and prey ratio. At the high drift rate (Fig. 7A), significant differences occurred among the ratios ($F_{2,12} = 8.98$; $P < 0.01$). Pairwise multiple comparisons (Tukey's T) showed that the OI at ratio 1:1 was significantly less than at ratios 2:1 and 5:1, but these latter were not significantly different from each other. The time effect was significant ($F_{5,60} = 67.12$; $P < 0.01$), but the ratio × time interaction was not. The outcome at the low drift rate (Fig. 7B) showed a similar pattern, with the OI averaging significantly lower at ratio 1:1 than at ratios 2:1 or 5:1.

When averaged over all ratios, the extent of optimization at the high drift rate (73.80) was considerably greater than at the low drift rate (57.38). This overall difference was significant at the 10% level ($F_{1,12} = 3.23$). Drift rate appeared to have its greatest effect at ratio 1:1 (cf. Fig. 7A and B). The optimization index appeared to reflect the combined patterns of predation on the three prey species (Fig. 4), particularly the greater mean response to large mealworms, earlier peak response to small crickets, and smaller contribution of brine shrimp at the high drift rate.

Discussion

Selective predation in brown trout appeared most directly related to prey size, distribution, and total abundance. Bisson (1978) found that prey size was the most important factor affecting prey vulnerability in drift-feeding rainbow trout. A simulation by O'Brien et al. (1976) suggests that, given more than one visable prey item, active selection by "apparent size" (prey length/distance to fish) provides the best explanation for predation by sunfish on *Daphnia*. This model would appear to require modification where significant opportunities for learning exist. For example, the distance from which rainbow trout attack prey increases not only with prey size, but also with experience (Ware 1972). I was unable to record reaction distances for brown trout but it seemed clear that these were not constant. Initially the fish moved several centimetres to capture brine shrimp; later I observed instances in which actual contact of brine shrimp with the snout failed to elicit a response.

Differential responses among prey species required several days to stabilize, and no prey were excluded from the diet. The learning processes considered in analyzing shifts in diet were (1) formation of a searching image ("learning to see," Tinbergen 1960), (2) development of a preference for specific kinds of prey (active "choice" among species, Krebs 1973), and (3) alteration of the area searched (movement into areas of "profitability" in terms of prey consumed/time, Royama 1970). The evidence did not suggest that sudden changes occurred in the predator's ability to detect the prey, i.e. search images were not apparent. Yet the experimental conditions probably minimized the role of detection. The three prey species were readily visible, edible, and necessarily passed through the fish's visual field. In natural streams where cryptic prey, turbid water, and constantly changing light conditions present a more demanding feeding situation, prey detection might become a significant, or even dominant, factor. My results do not refute the search-image idea; they simply show that prey selection in trout can also result from an active, differential response to the characteristics of the prey.

Variation in diets among individual trout was small, although differences in foraging behavior (e.g., feeding activity, body position) were sometimes evident. Bryan and Larkin (1972) have shown that individual trout may exhibit differences in their diet, evidently because of differences in searching technique, capturing technique, and feeding rhythm. Interaction among individuals may have played a role in bringing about specialization, as the authors observed frequent agonistic displays among fish. In my study little specialization was evident, perhaps because interactions with conspecifics were eliminated.

Brown trout apparently altered the area searched in response to prey density, which seems to support Royama's (1970) "profitability" hypothesis. Their continued capture of at least a few brine shrimp at all depths also supported the prediction of periodic sampling of all "niches." Ware (1972) suggests that rate of capture serves as an internal signal to control foraging behavior. My data do not provide a test of this idea in the context of drift feeding, but one might postulate that discrete rates of capture exist, beyond which foraging would be largely restricted to specific depths (prey concentrations).

Murdoch (1969) and Murdoch and Oaten (1975) have considered the stabilizing effect on community structure of "switching," which is defined as disproportionate predation on the most abundant prey species. Although brown trout were not actually subjected to changing prey ratios over time, comparison of their responses at ratios 1:1, 2:1, and 5:1 suggested that switching did not generally occur. The relationship between the proportion prey types consumed and the proportion available was roughly linear, i.e. preference (c) remained constant. Murdoch et al. (1975) examined data from a number of studies in terms of three generalizations about switching. The present study seems to support their second generalization, which is that if preference when prey are equally common is weak, but consistent among predators, then the predator should not switch. Of significance here is that, in brown trout, the preference "at equality" (ratio 1:1) was evidently based on prey size differences, rather than on differences in palatability or catchability.

An apparent exception to the general failure to switch was the initial (Day 2) disproportionate response to small crickets when these were five times as abundant as large mealworms. This phenomenon was most pronounced at the low drift rate, perhaps because preference was weaker at reduced levels of prey abundance (Murdoch et al. 1975). For most of the experimental period, large size discrepancies may have minimized the effect of prey abundance. While the available data do not rule out the significance of switching by brown trout, they do suggest that within a given area prey size may be more important than abundance in prey selection. If trout predation stabilizes prey communities, this may result mainly from movement into areas containing disproportionately high numbers of a prey species. In fact, the clearest documentation of switching in fishes (Murdoch et al. 1975) has involved predation by guppies (*Poecilia reticulata*) on two spatially separated species. As yet nothing is known of the ability of fishes to "anticipate" predictable patterns of prey availability (emergences), and the role of temporal heterogeneity in switching has not been investigated.

I did not attempt to quantify hunger within feeding periods, although this could be done in terms of gut capacity (e.g. Ware 1971). My observation of parallel shifts in response to the two larger prey types suggests that considerable change in stomach fullness may fail to be reflected in greater selectivity. The results seem to contrast with those of Ivlev (1961), who concluded that satiation was the mechanism that increased selectivity of carp (*Cyprinus carpio*). The apparent lack of effect of hunger on prey selectivity of brown trout, however, could have been caused both by an absence of differences in palatability between the prey types, and by the short duration of the daily sessions.

That experience can modify reaction distance (and thus prey selection) directly has been proposed by Ware (1971) to explain feeding behavior in rainbow trout. Similarly, Thomas (1977) proposed that, in addition to satiation effects, short-term positive and negative changes in motivation occur following "eat" and "reject" episodes, respectively. In sticklebacks these motivational effects appear to change both the search path and the probability of eating a particular item. Recent data (unpublished) suggest that short-term effects may also characterize brown trout feeding, particularly when prey species differ in palatability.

Ware (1972), Hansen (1972), and others have shown that predation rates can be stimulated by depriving fish of food for varying lengths of time. In systems where prey distributions are spatially discontinuous, a major role of hunger might be to regulate the rate of movement among microhabitats. Thus, Beukema (1968) found that in addition to increasing the number of complete responses to prey, higher hunger levels increased the swimming activity of sticklebacks. Presumably, nearly satiated trout would be least likely to move within the water column, and this could contribute indirectly to selective predation in drift feeders.

BROWN TROUT AS OPTIMAL FORAGERS

A basic hypothesis in most studies of optimal foraging is that net rate of energy intake will be maximized (Pyke et al. 1977). I assumed, provisionally, that equal energy expenditure was required in capturing the three prey species, and therefore, that total energy intake was an appropriate "currency" (Schoener 1971) to be maximized. Brown trout ultimately achieved as much as 91% of an hypothetical optimum diet in the laboratory. This required a relatively long period, during which familiarity was gained with new food types. The period was probably exaggerated by the short duration (30 min) of the feeding sessions. Although such brief periods of availability do occur in natural streams, this is the lower end of a spectrum extending to at least 5 h. Another factor that may have prolonged the approach to an optimum diet was the 3-wk exposure to brine shrimp before the sudden introduction of (energetically) more desirable prey. Nevertheless, the results suggest that models of prey selection need to incorporate the behavioral capabilities of predators, because the time to acquire an appropriate response can be appreciable.

Even after 800–1200 prey captures during 6 d the trout periodically sampled areas of low density, as well as species of low energy content. Such sampling appears to represent a "cost." Yet, leaving areas of high density permits sampling of areas where density may have recently become even higher. Within a given area, periodic sampling of even the least desirable prey (e.g. brine shrimp) may function to maintain the ability to respond rapidly to subsequent changes in abundance. Because of constraints imposed by the distribution of the prey and the behavioral capabilities of the predator, therefore, an optimal feeding strategy need not be directly reflected in a maximum energy intake. This generalization seems to complement the theoretical treatment by Pulliam (1974).

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Sensitivity Analysis of Two Harp Seal (*Pagophilus groenlandicus*) Population Models

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MOHN, R. K. 1979. Sensitivity analysis of two harp seal (*Pagophilus groenlandicus*) population models. J. Fish. Res. Board Can. 36: 404–410.

Sensitivity analysis has been used to estimate the relative importance of input parameters both between and within two harp seal (*Pagophilus groenlandicus*) population models. The population size at maximum sustainable yield is shown to be much more poorly defined than the yield level itself.

Key words: sensitivity analysis, harp seal, population model, sustainable yield, management

MOHN, R. K. 1979. Sensitivity analysis of two harp seal (*Pagophilus groenlandicus*) population models. J. Fish. Res. Board Can. 36: 404–410.

Nous avons utilisé l'analyse de sensitivité pour estimer l'importance relative des paramètres, à la fois interet intragroupes, de deux modèles de populations de phoques du Groenland (*Pagophilus groenlandicus*). Nous démontrons que la taille de la population au point de rendement maximal soutenu est beaucoup moins bien définie que le niveau de rendement lui-même.

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THE purpose of this paper is twofold. First the examination of two population models is undertaken using some techniques from systems theory, principally sensitivity analysis. The second object is to demonstrate the use of such techniques in general with suggestions for their application to other population models. Two models have been used recently to estimate seal herd population under various management strategies. They produce divergent estimates of sustainable yields and have different structures. One model (M1) has a single density dependent control, and a detailed description has not been published. Its performance and some details are reported in Capstick and Ronald (1976) and Capstick et al. (1976). The second model (M2) is described in Lett and Benjaminsen (1977). This reference contains A Programming Language (APL) listing for the model. To estimate parameter performance for each model, sensitivity analyses were carried out. They were performed over long (20-yr) periods to ensure that long-term effects would be visible, and short (4-yr) terms because management policies and new parameter estimates are usually reassessed within such a period.

In general, sensitivity analysis in an enquiry into the response of a modeled system to an incremental perturbation of initial conditions, inputs, parameters, or structure. The most familiar form of sensitivity is defined as the change in state variable caused by an incremental change in a controlling or descriptive parameter and this is the form we develop. Therefore inputs and initial conditions are kept constant and as similar as possible between models. Structural sensitivity, wherein the forms of the equation defining the model are changed, is most appropriate to the development of a model to find its "best" structure. As we are comparing existent models structural sensitivity was not undertaken. Rather the models are compared in terms of performance and parameter sensitivity.

The actual programs used in this study were coded by R.K.M. in Fortran. M1 is based upon a listing provided by C. Capstick (personal communication, University of Guelph, Guelph, Ont.) M2 is a Fortran version of the APL listing mentioned above. Care was taken to ensure that M1 and M2 reproduce the originals.

The general aspects of the exploited seal herd appear in each model. Both depend upon estimates of natural mortality, fecundity and pregnancy rates, catch levels, etc. They differ on the detailed level as will be discussed below. To afford grounds for comparison the starting population, adult catch and natural mortality estimate were used for both models.

Model M1

The single feedback model has evolved from Allen's (1975) work which has been in use since 1972. It offers a major feature that was not evaluated in this work, the use of a Leslie Matrix to produce a stable age distribution from an initial number of pups. This model

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TABLE 1. Starting population and pup production.

Age (yr)	Population animals	Pups (M1) animals	Pups (M2) animals	Age (yr)	Population animals	Pups (M1) animals	(Pups M2) animals
1	179 193	0	0	16	32 005	14 402	16 921
2	132 882	0	0	17	30 259	13 616	16 925
3	137 603	2 271	3 210	18	9 108	4 098	5 073
4	138 730	11 975	20 617	19	15 499	6 974	9 028
5	118 735	28 516	31 278	20	13 796	6 208	7 410
6	61 351	24 570	20 075	21	1 623	730	971
7	51 362	23 112	22 098	22	10 695	4 812	6 864
8	36 327	16 347	17 098	23	11 514	5 181	8 008
9	54 152	24 368	26 046	24	8 749	3 937	5 742
10	13 463	6 058	6 443	25	11 667	5 250	8 936
11	27 353	12 308	13 293	26	1 809	814	0
12	34 772	15 647	17 129	27	3 505	1 577	0
13	32 336	14 551	15 932	28	7 252	3 263	0
14	34 288	15 429	17 104	29	5 445	2 450	0
15	37 077	16 684	18 730	30	1 768	795	0
				Total	1252 550	285 956	316 941[a]

[a] M2 pup total plus 6% (see text) is 335 957.

simulates the population up to the age of 30. The population data used as a starting point for all simulations was derived from cohort analysis as reported in Lett and Benjaminsen (1977). As their modeled population is for ages 25 and under, five data were appended for ages 26–30 (see Table 1). The annual cycle for this model is outlined as

i) Scale harvest over population by age-group (pup, bedlamer, adult)
ii) Prepare output of population
iii) Subtract harvest
iv) Evaluate herd size of 1+ animals (THERD)
v) Calculate whelping rate (equations 1 and 2 below)
vi) Find pups born to 30 yr olds
vii) Apply natural mortality and age population
viii) Find pup production of remaining adults.
End of Loop.

The whelping rate (FEC) is either held constant at specified values or determined from the herd size by

$$C_{\text{mean}} = 3.997 + 0.845 \times 10^{-6}\,\text{THERD} \tag{1}$$

$$\text{FEC} = \text{Gauss}\,(\text{Age} - C_{\text{mean}})/1.118 \tag{2}$$

where Gauss is the probability function $P\ (X)$ and FEC, THERD, etc. are variable names used in the supplied program and C_{mean} is the mean age of whelping. Equation (1) is the result of a linear regression through three points and the ogive follows the probability function (see Fig. 1).

One of the options available in M1 is to run simulations without density-dependent feedback control on the whelping ogive. When density-dependent maturity was not required, data were used corresponding to Sergeant's (1976) estimates.

Model M2

This model is more complex than M1. It incorporates sex ratio data and the ability to undertake stochastic simulation. Stochastic is used in the sense that certain catch quotas and the natural mortality are drawn from normal distributions whose means and standard deviation are specified in the model.

The annual cycle in the model differs from the M1 with respect to phase and is principally

i) Split population into sexes
ii) Determine adult catch by sex
iii) Evaluate herd size N_t
iv) Calculate maturity and pregnancy rates (equations 3 + 4 below)
v) Find pup production
vi) Apply natural mortality adult + pups
vii) Update population.
End of Loop.

An important difference when compared to model M1 is the mechanism of the feedback control. Instead of the usual cumulative normal, a sinusoid constrained to the first quadrant was used to produce a maturity ogive, in original notation (see Fig. 1):

$$E_t = \sin\,(15522A - 2.245 \times 10^{-5} N_t - 16.017) \tag{3}$$

where A is age in years and E_t is fraction mature.

Also, if the population falls beneath a given level (1.002 million) the ogive ceases to translate. A second feedback control is constrained in this model, the pregnancy rate. This rate is linear with population size of animals age 2 and over, N_{2+}.

$$\text{Preg} = 1.048 - 9.746 \times 10^{-8} N_{2+} \tag{4}$$

These two mechanisms, working in series, greatly stabilize the model.

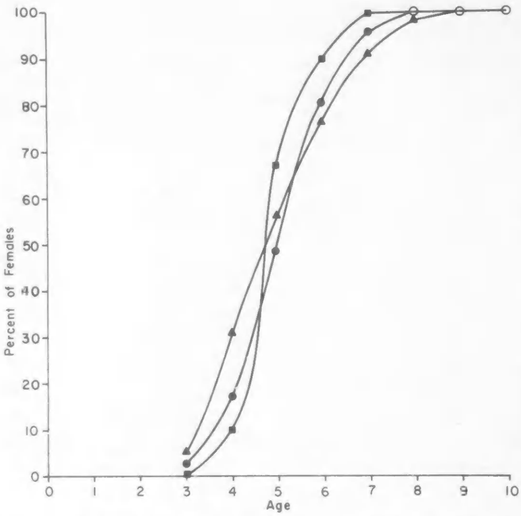

FIG. 1. Maturity ogives. ■, Sergeant's 1976 data; ●, M1 at initial population; ▲, M2 at initial population.

To compensate for modeled life span of 25 yr the pup production (Table 1) is multiplied by a factor of 1.06.

The principal effects observed when the simulations were averaged over 10 stochastic runs over a 20-yr period were a slight variation in sensitivities. It is concluded that using this stochastic ability has little effect on the relationship between the input parameters and the state variables.

The pup production for this model is significantly more than that of M1, ~50 000 animals for the population given in Table 1. M1 has a lower pregnancy rate, .9 compared to .95. It also assumes a 50:50 sex ratio while there are more females proportionally in M2. The maturity ogive for M1 is also lower at the abundant younger age-classes (Fig. 1). Finally M2 corrects for animals breeding over the age of 25 by adding 6% to the pup production, while M1 takes animals to age 30 and makes no correction for older females.

Analysis

We assume that the state of the modeled system is defined by a state variable, X. For these models X is either total or breeding population. The sensitivity S_i is the change in the state variable due to a change in the i^{th} input parameter P_i. In the limit of a small change in P_i and in the region of a reference value of X, X_r, we have

$$S_i = \frac{\partial X}{\partial P_i}. \tag{5}$$

In this region a change in only parameter P_i, say P_i will change X by X.

$$\Delta X = \frac{\partial X}{\partial P_i}\Delta P_i \tag{6}$$

Also, S_i may be approximated by

$$S_i \simeq \frac{X_i - X_r}{\Delta P_i} \tag{7}$$

where X_r is the value of state variable and all parameters are at reference level; X_i is the value of state variable all parameters at P^0 except P_i, the i^{th} parameter; ΔP_i is the change in i^{th} parameter for unperturbed level ($\Delta P_i = P - P_i^0$).

Miller (1974) based his analysis on a slightly different definition of sensitivity; the relative sensitivity (R_i) related a percentage change of an input parameter to a percentage change in the state variable. We will constrain our discussion to the simplest of a number of ways to do this.

Let $\Delta P_i = U_i P_i$, where the coefficient U_i is the percentage change of the i^{th} parameter, *e.g.* $U_i = 0.01$ represents a 1% change. To express the state variable change as a percentage we will divide it by its reference value X_r and multiply by 100, thus

$$R_i = \frac{X_i - X_r}{X_r}100 \quad \text{with} \quad \Delta P_i = 0.01P_i. \tag{8}$$

The relative sensitivity, R_i, as defined above is the percentage change in the state variable related to a 1% change in the i^{th} parameter. This relative sensitivity will be used in the majority of this study. It is a convenient form to use and is directly applicable to Miller's (1974) validation techniques. R_i is related to the S_i expressed in equation (7) by recalling that $\Delta P_i = 0.01\ P_i$ and R_i is a percentage.

$$S_i = R_i X_r / P_i. \tag{9}$$

A fundamental assumption of sensitivity analysis is that the state variable at any time is completely determined by the input parameters. Also, it is assumed that the parameters act in a linear manner and independently, at least over a small change. To demonstrate local linearity the relative sensitivities were determined for positive and negative 1% changes in the parameters. Another possible test would be to double, or increase by a given factor, the coefficient U_i and check the R_i for similar increases. The assumption is obviously not fulfilled in general for a feedback control system, such as a population model with density-dependent parameters. To check the assumption of independence for small changes all parameters are varied simultaneously, and the relative change from X_r recorded. This is compared to the predicted relative change, $\Sigma U_i R_i$. If the effects of parameters can be simply summed, e.g. act independently, the results will coincide. The U_i's for this test are not constrained to 1% but are drawn from a normal distribution with zero mean and a specified standard deviation.

This concept of predicted relative change in a state variable was expanded by Miller (1974) for validation of a model. If the coefficients U_i are equated to either estimated or assumed standard deviations, then the estimate of the standard deviation of the state variable, S_R, associated with the R_i is

$$S_R = \sum(U_i R_i)^2. \tag{10}$$

If this estimate is less than a level set by the investigator, the model is said to be valid.

The assumption of a completely deterministic system would appear to be contradicted by a stochastic model. But computer-generated random numbers were used to determine the stochastic values, resetting the seed or starting value before each determination of X ensures the same "path" is followed. The seed was therefore treated as an unvarying initial condition. Had this not been done the variances in the parameters, particularly natural mortality, would have dominated the variance due to a 1% parameter change as well as violating one of our assumptions.

The input parameters may be separated into two types. First are those that describe the modeled system, e.g. natural mortality. The second type relates to management policy, e.g. pup catch level. In either case sensitivity relates the amount of change expected in the output or state variable associated with a given change in an input. The descriptive type parameters in the model are not known exactly and have an associated error variance. The effect of the error of the inputs is an uncertainty related in the output. For very sensitive inputs the effect is larger. The management parameters are specified exactly, except of course those used in stochastic simulations, and sensitivities indicate how the state variable would respond if, for example, the catch did not equal a set quota or how critical are changes in one quota relative to another.

Although relative sensitivities are convenient when discussing errors in parameters or their effects, they may be misleading when comparing two models of the same system that have different internal structures or different definitions of parameters. An example of this is given below. Also, the classical sensitivity is useful in comparing management policies when the questions are formed as amounts rather than rates. For example, which would have the greater effect, an overrun of 5000 immature or 5000 mature animals in the catch? This example will be taken up again in the discussion.

Results and Discussion

The two models have been given as similar initial conditions as possible (Tables 2 and 3) and their performance compared. Starting from basically the same population, natural mortality, and adjusted harvest quotas, the pup production was first checked for differences (Table 1).

Before the sensitivity analysis was undertaken it was important that the models were operating under similar, stable conditions. Therefore, the pup quota was increased from 144 000 to 185 000 for the model M2. This ensured that both models were operating just beneath the sustainable yield point, i.e. the populations were growing very slowly.

TABLE 2. Unperturbed parameter values, model M1.

Parameter no.	Name	Value
1	Bedlamer harvest	24 000 animals
2	Adult harvest	12 000 animals
3	Pup harvest	144 000 animals
4	Constant eqn. (1)	3.9967 yr
5	Coeff. of herd size eqn. (1)	0.8450×10^{-6} yr/animal
6	Max. fecundity	0.9
7	Survivorship	0.905
8	Fecundity	As determined by eqn. (1) and (2) or given as data
9	Division eqn. (2) (SD)	1.118 yr

Figure 2 shows the results of the test for independence of parameters for model M2. The results for M1 are essentially the same. The X-axis is the percent change when the parameters are changed simultaneously and the Y-axis is the sum of the individual changes. The U_i were drawn with standard deviations of .5, 1, and 2%. The deviation from a line of unity slope is seen to be small indicating independence over small parameter changes.

The relative sensitivities for M1 are shown in Table 4. The dominant sensitivity is the survivorship, parameter 7. As one would expect this term is larger when the density dependence is not in effect. A comparison of the 20-yr runs with U_i positive and negative shows the model is locally linear with the exception of the survivorship and this is not surprising due to the magnitude of R_7. If we average the +1% and −1% values for

TABLE 3. Unperturbed parameter values, model M2.

Parameter no.	Name	Value
1	Adult harvest	36 000 animals
2	Pup harvest	185 000 animals
3	Natural mortality	$0.1\ \mathrm{yr}^{-1}$
4	Coeff. of age eqn. (3)	15.5223°/yr
5	Coeff. of herd size eqn. (3)	2.245×10^{-5}°/animal
6	Constant eqn. (3)	16.01743°
7	Constant eqn. (4)	1.048
8	Coeff. of herd size eqn. (4)	$9.7454 \times 10^{-8}\ \mathrm{animals}^{-1}$
9	Sex ratio in large vessel catch	As in Lett and Benjaminsen (1977)
10	Sex ratio initial population	As in Lett and Benjaminsen (1977)

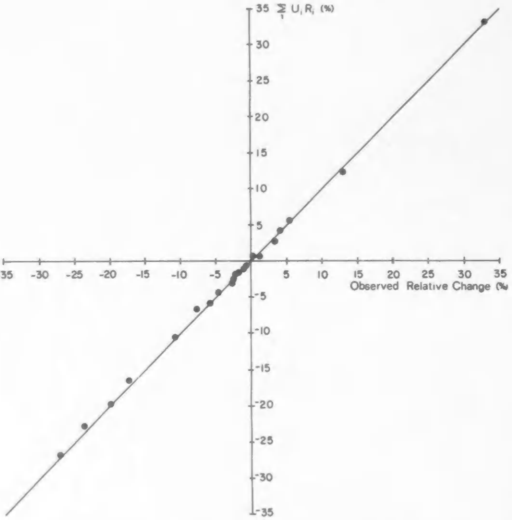

FIG. 2. Predicted and observed changes in total population for M2 while simultaneously and randomly varying all parameters.

R_7, the estimate is ~40%. This is to say that a 1% change in the survivorship causes approx. a 40% change in the total population after 20 yr with density-dependent maturity. The figure is higher if the density dependence is removed, as would be expected. The next largest sensitivity is R_8 with a value of 4.8%. Both P_7 and P_8 are parameters of the system descriptive type. The ratio of R_7 to R_8 is 8.3. When combining the effects of several parameters the variances are added and R's must be squared. Therefore, R_7 will have an 8.3^2 or 69 times larger a contribution to the total variance in the state variable if the error associated with P_7 is the same magnitude as the error associated with parameter 8. Of course these two parameters may have very different associated errors.

TABLE 4. Relative sensitivities R_i (%) model M1.

Density dep.	Yes	Yes	Yes	No
Period (yr)	10	20	4	20
U_i (%)	+1	−1	+1	+1
State variable		Total population		
Parameter no.[a]				
1	−0.666	0.665	−0.056	−0.693
2	−0.408	0.408	−0.033	−0.415
3	−2.397	2.385	−0.287	−2.500
4	−2.402	2.438	−0.256	0
5	−0.639	0.644	−0.068	0
6	3.772	−3.761	0.311	0
7	43.188	36.951	3.421	48.041
8	4.786	−4.763	0.421	5.236
9	0.056	−0.056	0.003	0
Reference	1282225	1282225	1239652	1493967

[a]See Table 2.

The relative sensitivities may be misleading when comparing two parameters within a model. Increasing the bedlamer harvest by 1% causes a 0.7% decrease in the population after 20 yr. Increasing the adult harvest by 1% decreases the population by 0.4%. One might infer from this that it is better for the herd to harvest more adults and fewer bedlamers while keeping the 1+ quota constant. This is not the correct conclusion. Using equation (9) we find the sensitivities

$$S_1 = \frac{-0.666 \times 1.28 \times 10^6}{2.4 \times 10^4} = -35.6$$

$$S_2 = \frac{-0.408 \times 1.28 \times 10^6}{1.2 \times 10^4} = -43.6.$$

These sensitivities, which will be called absolute to avoid confusion, show that the adult catch, P_2 actually has more of an effect per animal than the bedlamer catch. This is equivalent to correcting for the fact that 1% of the bedlamer catch respresents more animals than 1% of the adult.

The density-dependent or feedback control variable, the maturity ogive, is modeled to be linearly dependent upon herd size where P_4 is the constant and P_5 the coefficient of herd size (equation 1). The relative sensitivities show that the constant is more important. By way of analogy, a home heating system may be considered. Natural mortality is analogous to heat loss and reproduction rate to the heat produced by a furnace. In this analogy, the constant in equation (1) is related to the thermostat setting. In this light it is understandably important. The strength and linearity of the density dependence is reflected by the slope of the line relating the pup/adult to the index of the population size in Fig. 3. As expected M1 produces fewer pups, therefore this line is beneath those for M2. Also, the slope is of a smaller magnitude than those for M2, implying a weaker control.

Model M2 has its largest relative sensitivity related to P_7 (Table 5), the constant in the density-dependent pregnancy equation. The next two most important relative sensitivities are for the coefficient of age in the maturity relationship and natural mortality. Model M2 has two density-dependent controls, pregnancy and maturity. Large relative sensitivities seen in R_7 and R_4 indicate the importance of these controls. Figure 3 shows that the slope of M2 is ~2.5 times greater than that for M1. Note that when the effects of pregnancy control are removed by setting the pregnancy rate to a constant, the slope is still greater than that for M1. Thus two feedbacks alone do not guarantee a tighter control than a single feedback. It is important to consider the magnitudes also.

The change in sign in parameter 2 between 4- and 20-yr simulations observed when the breeding stock

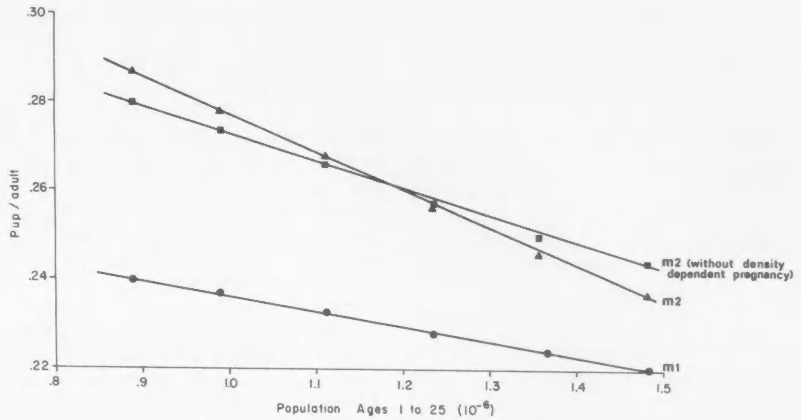

FIG. 3. Decline in pup production with population size. Slopes show strength of density-dependent control.

was used as the state variable, demonstrates the interdependence of the parameters. For example, decreasing the pup quota, P2, over a short span increases the breeding population, but over a long term naturally causes a decrease. This is because the simulated maturity ogive shifts immediately with the drop in population but the effects of the smaller production do not reach the breeding population for a few years. To ensure that this was not an artifact of an unstable age distribution in the population, the sensitivities were determined using the output of a Leslie Matrix as a starting population. The sign change was still evident, demonstrating this effect is due to the operation of the controls in the model.

With its tighter density-dependent control M2 offers a more precise estimate of the state variable in light of errors in management type parameters. But whether or not it is also more accurate cannot be answered with sensitivity analyses that relate changes in the state variable to changes in the input by definition. Errors in estimating parameters, especially descriptive parameters, may be thought of as indications of the probable change separating the estimated value from the unknown true value. And it is the accuracy of these estimates, derived from biological data, which determine the accuracy of estimates of the state variable. But sensitivity analysis can be of some use here also. If the sensitivity of one parameter were much higher than the others, it is an indication that an improvement in its estimate by expending more effort or money would have a larger effect in improving the accuracy of the model.

It is dangerous to make hasty conclusions using either relative or absolute sensitivities to compare models. For

TABLE 5. Relative sensitivities R_t (%) model M2.

Stochastic	No	No	No	Yes	No	No
Period (yr)	20	20	4	20	20	4
U (%)	+1	−1	+1	+1	+1	+1
State variable		Total population			Breeding females	
Parameter No.[a]						
1	−0.719	1.043	−0.108	−0.721	−0.340	−0.032
2	−2.439	2.392	−0.425	−2.627	−0.972	0.108
3	−3.196	3.204	−0.435	−3.320	−1.632	−0.188
4	3.102	−3.126	0.594	3.301	1.871	0.557
5	−1.206	1.216	−0.230	−1.269	−0.732	−0.204
6	−0.713	0.713	−0.136	−0.758	−0.432	−0.123
7	5.066	−5.206	0.886	5.425	3.050	0.882
8	−0.505	0.505	−0.807	−0.540	−0.308	−0.085
9	0.511	−0.513	0.024	0.555	0.343	0.047
10	2.914	−3.021	0.805	3.123	1.529	0.804
Reference	1240705	1240705	1196116	1142016	361905	356889

[a]See Table 3.

example, the relative sensitivity for survivorship is ~40% in M1, while that of natural mortality in M2 is 3.2, a ratio of 12.5. Thus for equal error variances, M1 appears to be 150 times more sensitive. These two parameters define the same concept, the exponential decay of the population with time. But natural mortality is the negative of the logarithm of the survivorship. The absolute sensitivites are

$$S_{7\,(M1)} = \frac{40.0 \times 1.28 \times 10^6}{0.905} = 5.7 \times 10^7$$

$$S_{3\,(M2)} = \frac{3.2 \times 1.5 \times 10^6}{0.1} = 4.0 \times 10^7.$$

The absolute sensitivity compensates for the different definitions of these parameters used by the original authors. Another approach would be to rewrite the programs, but it is better to leave them as close to the original form as possible to avoid errors, either in programming or interpretation. M1 is still seen to be more sensitive and this is corroborated by the smaller slope seen in Fig. 3.

A counter example is the coefficient of the herd size in the maturity relationship, P_5 in both models. The absolute sensitivities for these parameters are

$$S_{5\,(M1)} = \frac{-0.639 \times 1.28 \times 10^6}{0.845 \times 10^{-6}} = -9.7 \times 10^{11}$$

$$S_{5\,(M2)} = \frac{1.206 \times 1.25 \times 10^6}{2.245 \times 10^{-5}} = -6.7 \times 10^{10}.$$

This indicates that the density-dependent maturity rate is a stronger control in M1 and M2. However, the slopes in Fig. 3 show that M1 has less control than M2 with the pregnancy control defeated. The ratio of these slopes is about 1.8. This failure of the absolute sensitivities to reflect the magnitude of control is due to the subsequent operations on the product of herd size and P_5. M1 uses the product in the argument of a probability function after scaling by the standard deviation; M2 converts it from degrees to radians and then takes the sine. So in this case as the parameters have the same form, the coefficient of herd size in the equation for the maturity ogive, it is appropriate to compare S's.

To demonstrate the model validation procedure and to reveal an implication of the models' sensitivity to management, we recall that the variance of a state variable may be estimated by summing the products of the sensitivity and estimates of the various squares of each parameter, equation (10). Assume that the parameters investigated in M2 have the following associated standard deviation expressed as percentages: 5, 5, 10, 20, 10, 5, 10, 5, 5, which were felt to be reasonable (P. F. Lett, personal communication Bedford Institute, Dartmouth, N.S.). These values yield an estimated standard deviation of 81% for the population size and 47% for the size of breeding stock. Note that if the investigators responsible had imposed a limit of 50% expected relative error for the state variable population size, this model would be invalid. A starting population of 1.25 million and a catch near sustainability were used to determine these sensitivities. This is near the peak of the surplus yield curve in Lett and Benjaminsen (1977, figure 10). As the pup catch represents about 80% of the total kill, the estimated error of the state breeding stock is closely related to the expected error of a surplus yield level. Therefore, we infer that using such a model, the estimate of maximum sustainable yield, MSY, is much more precise than the estimate of the MSY population size.

We have investigated two models of harp seal populations. Methods for applying sensitivity analysis have been developed. Distinctions between relative and absolute sensitivities have been explored with examples to emphasize some pitfalls. Sensitivity analysis applied blindly may well lead to improper conclusions. As a rule of thumb, when comparing similarly defined parameters of identical function, the relative sensitivity is applicable. When comparing parameters of similar function but divergently defined the absolute sensitivity is probably more appropriate. Comparisons of relative sensitivities are more powerful if estimates of related error magnitudes are available to allow for estimates of the uncertainty of state variables or for model validation.

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Correlations Between *Daphnia magna* and Fathead Minnow (*Pimephales promelas*) Chronic Toxicity Values for Several Classes of Test Substances

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MAKI, A. W. 1979. Correlations between *Daphnia magna* and fathead minnow (*Pimephales promelas*) chronic toxicity values for several classes of test substances. J. Fish. Res. Board Can. 36: 411–421.

Chronic toxicity values were developed for *Daphnia magna* with six surfactants and a detergent builder, each selected on the basis of previously existing chronic fish test data. Predictive correlations were examined for testing end points between 21-d *Daphnia* chronics and 1-yr fish chronics to provide a short-term alternative chronic test species while developing toxicity data for an intermediate trophic level species. For the detergent materials tested, a strong correlation ($r = 0.98$) exists between *Daphnia* and fish no-effect concentrations. A replacement term, NOEC (no observed effect concentration), is suggested to clarify interpretive ambiguities associated with the definition of the MATC (maximum acceptable toxicant concentration) value. Additional chronic toxicity data from the current literature for these two test species and several test substances representing metals, polychlorinated biphenyl isomers, and pesticide formulations were similarly compared. A correlation analysis demonstrated an overall Pearson correlation coefficient of 0.79 for these data. Although significant outliers were evident from this correlation, these differences may be due primarily to differences in modes of toxic action of these test substances. The relatively short life cycle and 21-d duration of the test, small water volumes, ease in handling, high fecundity, and good correlation of 21-d chronic data with chronic fish toxicity data make *Daphnia* chronic tests an attractive alternative to the conduct of longer term fish tests.

Key words: Daphnia, Pimephales promelas, toxicity tests, chronic, mortality, surfactants, metals, pesticides

MAKI, A. W. 1979. Correlations between *Daphnia magna* and fathead minnow (*Pimephales promelas*) chronic toxicity values for several classes of test substances. J. Fish. Res. Board Can. 36: 411–421.

Nous avons établi les valeurs de toxicité chronique à l'endroit de *Daphnia magna* de six substances tensioactives et un renfort de détergent, chaque substance ayant été choisie sur la base de données obtenues dans des essais antérieurs de toxicité chronique avec des poissons. Nous examinons les corrélations prévisionnelles pour trouver les fins de réactions des *Daphnia* après 21 d et des poissons après 1 an de toxicité, et ceci dans le but de trouver une autre espèce pour essais de toxicité chronique à court terme, tout en obtenant des données sur la toxicité à l'endroit d'une espèce de palier trophique intermédiaire. Pour ce qui est des matériaux détersifs testés, il existe une forte corrélation ($r = 0{,}98$) entre les concentrations dénuées d'effet pour les *Daphnia* et celles des poissons. Nous suggérons un autre terme, NOEC (concentration dénuée d'effet observable), afin de clarifier les ambiguïtés d'interprétation associées à la définition de la valeur de la MATC (concentration maximale acceptable de toxique). Nous avons comparé de la même manière d'autres données de toxicité chronique extraites des publications courantes concernant ces deux espèces et plusieurs substances testées, représentant des métaux, des isomères de biphényls polychlorés et diverses formules de pesticides. Une analyse de corrélation donne, pour ces données, un coefficient général de corrélation de Pearson de 0,79. Bien que cette corrélation révèle des divergences importantes, ces dernières peuvent résulter surtout de différences dans le mode d'action toxique des substances testées. Les essais chroniques avec *Daphnia* sont une alternative attrayante aux essais à plus long terme avec des poissons, pour les raisons suivantes : cycle biologique relativement court de même que la durée de l'essai, 21 d, faibles volumes d'eau, facilité de manutention, haute fécondité et bonne corrélation entre les données de toxicité chronique de 21 d et celles des poissons.

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THE use of laboratory toxicity tests with aquatic species is the backbone of current efforts to develop aquatic safety assessments and establish water quality criteria for new chemicals and materials potentially reaching the aquatic environment. In constructing laboratory dose–response relationships for aquatic species, one of the more important testing end points has become the determination of the maximum acceptable toxicant concentration (MATC) originally proposed by Mount and Stephan (1967) and defined as the highest test concentration at which no effects are observed on survival, growth, or any of the reproductive parameters examined during the full life cycle exposure.

The acronym MATC is somewhat ambiguous. Because it is neither a maximum, nor necessarily acceptable, and not always related to a toxicant, it is appropriate to propose the adoption of a replacement term. In practice, the maximum concentration causing no effects on the test organisms is related to the dilution series the investigator chooses to employ in the toxicity test. The *actual* maximum concentration causing no effects lies somewhere between the lowest observed effect concentration and the highest observed no-effect concentration unless the investigator has been extremely fortunate in selecting exposure concentrations. Thus the test results report only an observed no-effect concentration as an estimate of the *actual* maximum no-effect concentration. The term acceptable implies the element of risk analysis and requires subjective judgmental decisions often beyond the responsibilities of the laboratory investigator. Also, the chronic test is often done with chemical substances that are not classified as toxicants but that require long-term exposure data for a complete hazard evaluation. For these reasons NOEC (no observed effect concentration) is proposed as a logical replacement term for MATC implying no change in the manner of determining the concentration but simply a clarification of its interpretive significance.

The chronic testing concept was originally developed with the fathead minnow, *Pimephales promelas*, and subsequent investigators have come to rely heavily on the fathead as the species of choice for chronic toxicity tests. Its advantages are generally listed as relatively short life cycle (10–12 mo), readiness to spawn within the laboratory, and ease of handling eggs and fry. However, these same features can also be listed as disadvantages depending on one's frame of reference. For example, the cladoceran *Daphnia magna* offers an extremely short life cycle reaching reproductive maturity within only 8 d. The species is extremely prolific, producing as many as 20–30 young per day from a single mature individual. Life cycles and reproductive parameters are relatively consistent between individuals, creating a good statistical basis for description of effects. The additional advantages of small water volumes and miniaturized testing apparatus make this invertebrate an extremely desirable test species for aquatic toxicologists.

Daphnia magna has been recognized for many years as a useful test species (Anderson 1944) and its sensitivity to chemical substances has been recognized as generally representative of other widely distributed zooplankton species (Anderson et al. 1948). Information extending comparisons between *Daphnia* NOEC values and those reported for fish is limited to a series of five metal ions (Biesinger and Christensen 1972), indicating that estimated full life cycle no-effect concentrations for Cr^{++}, Cu^{++}, and Zn^{++} to daphnids were similar to those for gammarids and fish, even though different metal salts, water hardness, and dilution water quality were used. However, Ni^{++} and Cd^{++} were found to be more toxic to *D. magna* in soft water than to fathead minnows in hard water, and comparative assays in waters of similar quality are not available.

The objectives of this investigation were threefold: (a) develop a laboratory procedure for the continuous-flow toxicity testing of *Daphnia* that would allow the maintenance of expected nominal test concentrations of highly degradable surfactants throughout the 21-d chronic test, (b) develop a data base for several representative surfactant materials to serve as a comparison of observed *Daphnia* effect concentrations with existing chronic values for fish species, and (c) extend these comparisons to other classes of chemical substances through a review of the current literature.

Materials and Methods

TEST SYSTEM

A modified 0.5-L proportional diluter (Maki 1977) is used to deliver predetermined concentrations of test material to the mixing cells where food is added via a six-channel peristaltic pump and the cell contents drained through the siphon tube to the flow-splitter box (Fig. 1). The flow-splitting box is drained through four 2.5-cm sections of 1 mm OD capillary tubing to restrict rate of flow to the test chambers, which are 1-L beakers with a 2.5 × 5 cm notch covered with a portion of 60-mesh stainless steel screen to prevent escape of newly produced young. The food material consists of a 1000 mg/L suspension of ground trout chow and alfalfa (Biesinger and Christensen 1972) and is renewed daily. Dilution water used for all *Daphnia* tests is carbon and reverse osmosis filtered well water (Table 1).

TEST CONDUCT

All test beakers are filled with the appropriate concentrations of test material by manually operating the diluter through consecutive cycles before adding young. The test is set up with *Daphnia* <12 h old. The young are siphoned from culture units and randomly assigned to test containers. Five young are used in each of the four replicates, thus yielding 20 F_0 individuals in each of the five test concentrations and controls. F_0 mortality is recorded after 24 h, 96 h,

TABLE 1. Dilution water quality for all *Daphnia* chronic tests with surfactants.

Parameter	Concentration (mg/L)
Hardness	120 mg/L Ca CO_3
pH	7.4±0.2
Dissolved oxygen	8.5±9.5
Nitrate	<0.05
Nitrite	<0.05
Copper	<0.001
Iron	<0.05
Lead	<0.01
Sodium	11.6
Zinc	<0.001

7 d, and thereafter on a daily basis. Production of the second generation usually begins on day 7 or 8 and all young produced are counted and discarded daily. Records are kept of the total number of F_0 surviving at each observation day, the total number of F_1 young produced by the F_0 individuals after reaching reproductive maturity, the mean brood size as the quotient of F_1/F_0, and the percentage of days that young were produced within each replicate beaker of all five test concentrations and controls.

Initial measurement of pH, temperature, and dissolved oxygen are taken immediately after inoculation. Also, at this time a water sample is removed from the beaker and preserved with either 1% formaldehyde for anionic surfactants or H_2SO_4 to pH 2 for nonionics and kept at 5°C before analytical confirmation of the nominal test concentrations. A continuously reading probe provides a constant record of water temperature throughout the test. All tests are run at 21 ± 1°C and additional analyses of test material, pH, and dissolved oxygen are taken at intervals of 3–5 d for the remainder of the 21-d test.

Six surfactants and a detergent builder as characterized in Table 2 were selected for testing on the basis of previously existing full or partial chronic test data for the fathead minnow, *P. promelas.*

Water samples were analyzed by MBAS (APHA 1977) for anionic surfactants and CTAS (Boyer et al. 1977) for nonionics to confirm expected nominal test concentrations. Type A zeolite was analyzed by the silicate method (APHA 1977).

STATISTICAL ANALYSIS

All results were calculated with a computerized probit analysis program (Finney 1964, 1971). Survival data for 96 h and 21 d was used to calculate LC50 values and associated 95% confidence intervals. Data for the three measurements of reproductive inhibition including total young production, mean brood size, and percentage of days that reproduction occurred was converted to percent effects, considering unexposed controls for each test as 0% effects. Respective EC50 values denoting the test concentration where a 50% reproductive inhibition was observed were also calculated with the probit analysis program. All calculations were based on mean measured concentrations of test material taken from the test containers during the 21-d test period. NOEC values for all test materials were determined as the highest measured test concentration causing no perceptible effects on all parameters of survival, growth, and reproductive performance relative to control data.

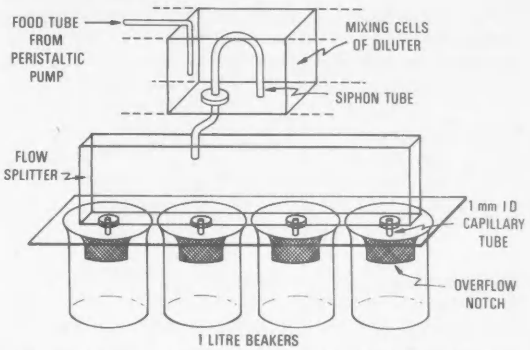


FIG. 1. Four-way flow splitting device for conduct of continuous flow chronic toxicity tests with *Daphnia.*

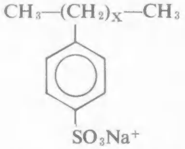
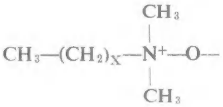
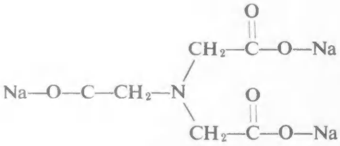
Results

An example of the type of chronic data generated during a typical 21-d *Daphnia* test is summarized in Table 3. These data for the nonionic surfactant, C_{12-13} alkyl ethoxylate, indicate that 21-d survival of initial F_0 individuals is significantly reduced relative to control survival in concentrations in excess of 0.4 mg/L. Measurements of reproductive inhibition indicate that the cumulative total young production and the mean daily brood size are both markedly reduced relative to control production in concentrations in excess of 0.24 mg/L. The percentage of days that reproduction occurred within each test concentration relative to controls was not affected until mean concentrations of the surfactant exceeded 0.81 mg/L, indicating that this measurement is apparently a less sensitive indicator of chronic toxicity than are the other measurements of total young production and mean brood size.

A summary of the calculated 50% effect levels for survival and reproduction of *Daphnia* populations under continuous-flow exposures to the six surfactants and one builder demonstrates similarities in responses of the test organisms to these materials (Table 4). A comparison of acute effect data for 96 h and 21 d demonstrates the expected directional increase in toxicity following the longer exposure period. However, the magnitude of this difference is not great for the majority of these materials since the 95% confidence limits overlap for four of the compounds, thus indicating that cumulative toxicity is apparently not significant for these surfactants or the builder.

An examination of the reproductive inhibition data demonstrates that the total number of young produced by *D. magna* is the most sensitive indicator of chronic toxicity. The EC50 values for total young production are uniformly the lowest effect concentrations measured

TABLE 2. Chemical characterization of the test surfactants and single builder. Generic names are used throughout text to refer to the test materials.

Generic name	Structure	Chemical characterization
$C_{11.8}$ LAS		Anionic, mean alkyl chainlength = 11.8, range C_{10-14}; mean phenyl position = 3.76; mean molecular weight = 345
C_{13} LAS		Anionic, mean alkyl chainlength = 13.3, range C_{10-14}; mean phenyl position = 4.5; mean molecular weight = 367
Alkyl ethoxylate sulfate	$CH_3—(CH_2)_X—O(C_2H_4O)_YSO_3Na$	Anionic, X = 13.67; range = 13–15 Y = 2.25; molecular weight = 425
$C_{14.5}$ alkyl ethoxylate	$CH_3—(CH_2)_X—(C_2H_4O)_YH$	X = 7 to 19, mean = 13.5 Y = 0 to 12, mean = 7.0 Nonionic
$C_{12.5}$ alkyl ethoxylate		X = 7 to 19, mean = 11.5 Y = 0 to 12, mean = 6.5
Amine oxide	 $CH_3—(CH_2)_X—\overset{CH_3}{\underset{CH_3}{N^+}}—O—$	Nonionic, alkyl dimethyl amine oxide molecular weight = 243 X = mean 11.7
NTA		Builder, trisodium nitrilotriacetate molecular weight = 257
Type A zeolite	$Na_{12}[(AlO_2)_{12}(SiO_2)_{12}]\cdot 27HOH$	Mean particle size = 3 μm Al:Si molar ratio = 1:1

for all seven test compounds. The average brood size, calculated as the number of young removed daily from each test container divided by the total number of adults present, yields EC50 values slightly higher than total young production and with generally wider confidence intervals due to the high variability in the day to day production of young from individual *Daphnia*.

Similarly, the measurement of the percentage of days that reproduction occurred, defined as the relative percent or frequency of days that young production was observed within the beaker compared to controls, yields still higher individual variances in brood production data. On any given day it is likely that at least one of the remaining test adults per container will produce a brood of young which is then recorded as a day on which reproduction occurred. Thus the EC50 values calculated for this parameter are generally higher than the other measurements of reproductive inhibition.

All 50% effect levels for both survival and reproductive inhibition are lower for C_{13}LAS (linear alkyl benzene sulphonate) than for $C_{11.8}$LAS, indicating that the addition of an average of 1.2 alkyl carbons creates an approximate 50% increase in toxicity for these anionic surfactants. A similar comparison of test results between C_{12-13} and C_{14-15} alkyl ethoxylates demonstrates the longer chain length compound exerts a greater toxic effect for all life cycle parameters measured. The chronically toxic concentrations of the alkyl ethoxylate sulfate and amine oxide are comparable to the concentrations exerting chronic effects for C_{12-13} alkyl ethoxylate with the exception that the concentration of amine oxide producing an inhibitory effect on reproduction are significantly higher than the alkyl ethoxylates. Data for the builder, Type-A zeolite, indicates suspensions of this insoluble compound are relatively nontoxic to daphnids in concentrations below 200 mg/L.

FATHEAD MINNOW CHRONICS

A summary of chronic toxicity data for eight test materials indicates similarities in relative toxicity of these materials with the *Daphnia* data (Table 5). The longer alkyl chain length, C_{13}LAS, is again more toxic to the fathead minnow than the $C_{11.8}$LAS by approximately tenfold. Although no effects were observed for $C_{11.8}$LAS at the highest test concentration of 1.09 mg/L under hard water conditions of 200 mg/L

TABLE 3. A summary of typical survival and reproductive performance data for populations of *Daphnia magna* exposed to the nonionic surfactant C_{12}–C_{13} alkyl ethoxylate.

	Test concn (mg/L)					
Day of test	Control	0.15	0.24	0.4	0.81	1.45
Number of individuals surviving						
0	20	20	20	20	20	20
1	20	18	20	19	20	16
2	19	18	17	18	19	7
4	19	18	17	16	18	3
5	19	17	17	16	17	1
7	19	17	17	16	15	0
9	19	17	17	16	15	0
12	19	17	17	16	15	0
14	19	17	17	16	15	0
16	18	17	17	16	15	0
19	18	15	16	16	14	0
21	18	15	16	16	14	0
Total young production						
9	42	117	129	58	5	0
12	174	222	282	92	0	0
14	134	156	98	117	0	0
16	451	434	383	166	0	0
19	771	434	683	436	0	0
21	238	209	249	436	0	0
Totals:	1810	1572	1779	1305	5	0
Mean brood size						
9	2.6	6.9	7.6	3.6	.03	0
12	10.9	13.1	16.6	5.8	0	0
14	8.3	9.2	5.8	7.3	0	0
16	28.2	25.5	22.5	10.4	0	0
19	48.2	28.9	39.9	27.3	0	0
21	15.9	13.9	15.6	27.3	0	0
Grand means	19.0	16.3	18.0	13.6	~0	0
Percentage of days reproduction occurred						
Replicate						
A	83	83	67	100	17	0
B	83	100	67	100	17	0
C	83	83	83	83	0	0
D	83	100	100	83	0	0
Means:	83	91.5	79.3	91.5	8.5	0

$CaCO_3$, larval survival was impaired in a similar test at 0.74 mg/L $C_{11.8}$LAS when tested in soft water of 39.0 mg/L $CaCO_3$. Results of these two tests then yield an NOEC of 0.90 mg/L $C_{11.8}$LAS when interpolated to the 120 mg/L hardness level at which the *Daphnia* tests were completed.

Results of a fathead minnow full chronic exposure to the nonionic C_{12-13} alkyl ethoxylate indicate no effects on all parameters measured at the highest test exposure of 0.32 mg/L which thus constitutes the NOEC value. Although no effects on spawning or egg production were observed at all test concentrations of alkyl ethoxylate sulfate, the highest test concentration did produce significant growth effects. Thus the NOEC is defined as the second highest exposure of 0.10 mg/L. Similarly, no effects on spawning or egg production were observed at all test concentrations of amine oxide; however, the percent hatch of F_1 larvae was reduced at the highest concentration of 0.86 mg/L therefore indicating an NOEC of 0.50 mg/L.

The full chronic exposure of the fathead minnow to NTA indicated no effects on growth, survival, or reproduction at all concentrations tested as high as 53.9 mg/L in soft water of 45 mg/L $CaCO_3$ (Arthur et al. 1974). Since the toxicity of NTA is a direct function of water hardness, becoming less toxic in waters of increasing hardness (Biesinger et al. 1974), it is reasonable to extrapolate these results to the 120 mg/L hardness concentration under which the *Daphnia* exposures were completed. Using this relationship, the NOEC for NTA was determined to be 75.0 mg/L in waters of 120 mg/L hardness.

Data for C_{14-15} alkyl ethoxylate and Type-A zeolite are the results from 30-d partial chronic or embryo–larval tests (Table 5). The majority of available data for a wide variety of test materials indicate that concentrations of test materials safe to fish over their entire life cycle can be estimated from the results of these 30-d continuous exposures of embryos and newly hatched fry (Macek and Sleight 1977). Therefore results from these two tests are used as estimates of chronic fish toxicity for purposes of comparison with the chronic *Daphnia* data. Thirty-day larval survival was reduced in the highest two exposures to C_{14-15} alkyl ethoxylate and survival in all remaining concentrations was statistically indistinguishable from control survival at $P = 0.05$ thus indicating an NOEC of 0.18 mg/L. Results of the fathead minnow embryo–larval exposure to relatively nontoxic Type-A zeolite indicate no effects at any test concentration up to 86.7 mg/L. These data along with other extensive toxicity studies including several marine and freshwater fish species have been summarized (Maki and Macek 1978). All data indicate that the material is nontoxic to fish species at concentrations >780 mg/L and actual NOEC values probably exceed these concentrations.

Discussion

SURFACTANTS

The test results demonstrate that *D. magna* can be used as an indicator of chronic toxicity for various surfactants and the detergent builder, Type-A zeolite. A measurement of survival and total number of young produced following a continuous 21-d exposure to the test materials yields an estimate of *Daphnia* survival potential and reproductive inhibition. From these test results it is possible to report NOEC values for *Daphnia* based on 21-d no-effect concentrations. These values are then compared to NOEC values for the fathead minnow, *P. promelas* (Table 6). Published NOEC values for NTA were added to this table to extend the comparison. It is important to emphasize that these

TABLE 4. Concentrations (mg/L) of six surfactants and a detergent builder that affect the survival, growth, and reproduction of *Daphnia magna* under continuous-flow testing conditions. Numbers in parentheses denote confidence limits for $P = 0.05$.

			Reproductive inhibition EC50 (mg/L)		
Material	96-h LC50	21-d LC50	Total young production	Average brood size	Percentage of days reproduction occurred
$C_{11.8}$ LAS	3.94 (2.87–6.83)	1.67 (1.28–2.18)	1.50 (0.75–3.33)	2.30 (1.62–3.55)	2.31 (0.30–4.18)
C_{13} LAS	2.19 (1.85–2.82)	1.17 (0.96–1.39)	1.11 (1.03–1.18)	1.41 (1.33–1.50)	1.29 (1.21–1.37)
C_{12-13} alkyl ethoxylate	1.14 (0.96–1.31)	0.93 (0.75–1.13)	0.46 (0.43–0.53)	0.47 (0.44–0.53)	0.70 (0.51–0.76)
C_{14-15} alkyl ethoxylate	0.43 (0.37–0.51)	0.37 (0.32–0.44)	0.28 (0.27–0.29)	0.29 (0.28–0.30)	0.33 (0.30–0.36)
Alkyl ethoxylate sulfate	1.17 (0.82–1.66)	0.74 (0.56–0.94)	0.37 (0.22–0.54)	0.40 (0.23–0.60)	0.52 (0.31–0.76)
Amine oxide	1.01 (0.85–1.21)	0.96 (0.90–1.03)	0.88 (0.77–1.04)	1.01 (0.95–1.07)	1.04 (0.98–1.11)
Type A zeolite	377.17 (315.30–464.83)	214.63 (174.27–256.17)	211.29 (177.89–255.66)	340.97 (281.79–412.57)	312.70 (272.89–369.04)

test data were all developed under continuous-flow conditions with every attempt to maintain maximum concentrations of the undegraded surfactant. In the present context, the method does not yield data for the assessment of effects of actual environmental forms of these test materials since numerous ameliorative environmental mechanisms are known to reduce significantly the acute and chronic toxicity of these surfactants. Following use and discharge to wastewater collection systems, rapid biodegradation by natural bacterial flora and adsorption to suspended solids combine to reduce the toxicity of the surfactant molecule to a fraction of the undegraded free form. Further biodegradation occurring within wastewater treatment facilities has been shown to eliminate measurable toxicity (Maki et al. 1978).

A close agreement between the *Daphnia* and fathead minnow NOEC values is obtained for the eight test materials. A regression analysis indicates a strong relation exists (Fig. 2); $r^2 = 0.98$ for the straight line equation.

Employing the equation it is theoretically possible to calculate chronic NOEC values for the fathead minnow given the NOEC value for *Daphnia* derived from a 21-d chronic exposure. Although this relationship is based on only eight test compounds, the relatively good agreement between chronic NOEC values for these two species lends support to the extension of *Daphnia* data to fish species.

OTHER TEST SUBSTANCES

To examine the extent of this relationship for a wider variety of test substances potentially reaching natural surface waters, an extensive review of the available literature summarizing toxicity data for the fathead minnow and *Daphnia* was conducted. Numerous published and unpublished reports from several testing laboratories were reviewed to develop the data base for this comparative evaluation. It is somewhat of a commentary on the evolving field of environmental science in general and, specifically, on the relatively

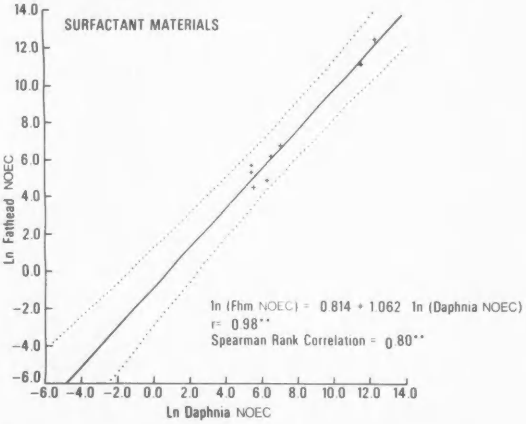


FIG. 2. Linear regression of no observed effect concentrations (NOEC) from chronic *Daphnia* and fathead minnow toxicity tests with eight detergent components. $^{**}P \leq 0.01$; ln (Fhm NOEC) = ln of the fathead minnow NOEC value; ln (*Daphnia* NOEC) = ln of *Daphnia* NOEC value.

young science of aquatic toxicology, to note that we were able to locate only 27 materials for which chronic tests had been completed for both *Daphnia* and the fathead minnow. The data were sorted into four major categories of test materials, analyzed separately using regression equations and correlation coefficients, and secondly, recombined with our in-house data for six surfactant materials and one builder (Table 7). Care was taken to check the similarity of water quality of the dilution media and other physical–chemical variables that may affect the behavior and subsequent toxicity of the test materials. The three major classes of test substances for which comparative data were available included PCB isomers, metals, and several pesticide formulations (Table 7). Where chronic no-effect concentrations were expressed as a range between two successive test concentrations, a single mid-range concentration was selected from this range to allow a direct statistical comparison of the single values for both fathead minnows and *Daphnia*. Regression equations for ln (NOEC) from both species were calculated using the computerized PROC CORR Program (Barr et al. 1976). The Pearson correlation coefficient testing the significance of the overall correlation, the Spearman Rank correlation coefficient testing the sig-

TABLE 5. Chronic toxicity summary for the eight test materials and the fathead minnow.

Mean measured concn (mg/L)	Number of females	Number of spawnings	Total eggs produced	Number of eggs per female
$C_{11.8}$ LAS				
1.09	19	37	3 616	190
0.53	8	37	3 131	391
0.25	14	60	7 531	538
0.12	15	27	2 020	135
0.06	12	33	2 169	181
Controls	19	19	2 401	126
C_{13} LAS				
0.25	13	3	86	7
0.10	9	22	1 211	135
0.06	12	36	4 148	346
0.03	11	13	791	72
0.02	12	27	2 652	221
Controls	14	63	7 425	530
C_{12-13} alkyl ethoxylate				
0.32	17	51	5 062	298
0.26	15	50	3 310	221
0.15	16	72	6 382	399
0.10	17	77	6 103	359
0.10	15	40	3 637	243
Controls	18	32	2 186	122
Alkyl ethoxylate sulfate				
0.22[a]	7	39	4 551	650
0.10	8	39	4 003	501
0.05	17	97	7 605	446
0.02	16	54	3 580	224
0.01	15	37	1 995	133
Controls	19	106	8 156	429
Amine oxide[b]				
0.86	19	86	14 102	742
0.50	10	60	5 991	599
0.24	12	84	7 816	651
0.13	10	30	2 182	218
0.08	12	53	6 348	529
Controls	11	14	1 606	146
NTA[c]				
53.9	9	75	9 496	1055
17.9	14	133	20 083	1434
8.7	8	67	10 105	1263
4.3	15	75	8 787	586
2.1	18	140	19 177	1065
Controls	17	94	11 956	703

TABLE 5 *(Concluded)*

Mean measured concn (mg/L)	Mean hatch %	30-d survival %	Mean total length (+1 SD)
C_{14-15} alkyl ethoxylate[d]			
0.26	72	0	—
0.20	88	2	19±2.8
0.18	84	41	15±1.4
0.11	84	66	16±2.3
0.07	88	49	15±2.1
Controls	87	52	16±2.1
Type A zeolite[d]			
86.7	91	96	18±2.0
22.6	92	96	18±2.0
12.3	93	88	19±1.0
6.2	93	92	20±2.0
Controls	91	98	18±2.0

[a] Growth effects observed at highest concentration.
[b] Percent hatch of F_1 reduced at highest concentration.
[c] Arthur et al. 1974.
[d] Partial chronic exposures.

TABLE 6. Comparison of chronic toxicity values (NOEC) for *Daphnia* and fathead minnows for several surfactants and two detergent builders.[a]

Test material	NOEC values (mg/L)	
	Daphnia	Fathead minnow
$C_{11.8}$ LAS	1.18	0.90
C_{13} LAS	0.57	0.15
C_{12}-C_{13} alkyl ethoxylate	0.24	0.32
C_{14}-C_{15} alkyl ethoxylate	0.24	0.18
Alkyl ethoxylate sulfate	0.27	0.10
Amine oxide	0.70	0.50
Type A zeolite	200.0	175.0
NTA	100.0[b]	75.0[c]

[a] Concentrations of undegraded parent surfactant molecules do not reflect significantly reduced toxicity of the actual biodegraded environmental forms of these materials.
[b] Biesinger et al. 1974.
[c] Arthur et al. 1974.

TABLE 7. Comparison of chronic toxicity values (NOEC) for *Daphnia* and fathead minnows for several metals, PCB isomers, and pesticide formulations.

	Fhm NOEC[a]	Reference	*Daphnia* NOEC[a]	Reference
Metals				
Cadmium	40.0	Pickering & Gast 1972	0.2	Biesinger & Christensen 1972
Chromium	350.0	Pickering 1977	330.0	Biesinger & Christensen 1972
Copper	17.0	Mount & Stephan 1969	22.0	Biesinger & Christensen 1972
Methylmercury	0.1	Mount & Olson 1977	0.14	Biesinger et al. 1977
Nickel	400.0	Pickering 1974	30.0	Biesinger & Christensen 1972
Zinc	80.0	Brungs 1969	70.0	Biesinger & Christensen 1972
Zinc	85.0	Benoit & Holcomb 1977	70.0	Biesinger & Christensen 1972
PCB isomers				
1242	15.0	Nebeker et al. 1974	20.0	Nebeker & Puglisi 1974
1248	1.3	DeFoe 1977	1.0	Nebeker & Puglisi 1974
1254	1.9	Nebeker et al. 1974	1.0	Nebeker & Puglisi 1974
1260	4.0	DeFoe 1977	10.0	Nebeker & Puglisi 1974
Pesticides and other materials				
Acrolein	26.5	Macek et al. 1976a	25.5	Macek et al. 1976a
Atrazine	230.0	Macek et al. 1976c	220.0	Macek et al. 1976c
Baygon	400.0	Macek et al. 1977	28.2	Macek et al. 1977
Diazinon	8.0	Allison & Hermanutz 1977	0.24	Biesinger 1973
Endosulfan	0.3	Macek et al. 1976a	3.0	Macek et al. 1976a
Heptachlor	1.5	Macek et al. 1976a	15.0	Macek et al. 1976a
Lindane	16.5	Macek et al. 1976b	15.0	Macek et al. 1976a
Malathion	250.0	Mount & Stephan 1967	0.57	Biesinger 1973
Methomyl	375.0	Macek et al. 1977	3.75	Macek et al. 1977
Nitroglycerine	80.0	Bentley et al. 1976	3000.0	Bentley et al. 1976
Phosphorus (P_4)	0.38	Bentley et al. 1976	5.0	Bentley et al. 1976
Propachlor	170.0	Macek et al. 1977	1000.0	Macek et al. 1977
RDX	1700.0	Bentley et al. 1977	2800.0	Bentley et al. 1977
Sevin	300.0	Carlson 1971	8.0	Biesinger 1973
Trifluralin	3.0	Macek et al. 1976a	3.5	Macek et al. 1976a
Halogens				
Chlorine	16.5	Arthur & Eaton 1971	3.0	Arthur 1971

[a] NOEC value expressed as μg/L.

nificance of the individual rankings, and level of significance of each were also calculated following this procedure.

METALS

Data available for six metals and one organometallic (Table 7) were combined and the correlations were statistically significant (Fig. 3). The majority of the metal chronic studies with the fathead minnow have been completed in relatively hard well water (~200 mg/L $CaCO_3$) at the USEPA Newtown Fish Toxicology Station near Cincinnati, Ohio, while the *Daphnia* chronics were all completed at the USEPA Environmental Research Laboratory at Duluth, Minn., using relatively soft Lake Superior water (~50 mg/L as $CaCO_3$). Since it has been well established that metal toxicity is strongly influenced by water hardness, being most toxic in soft waters, it is reasonable to assume that the data for these metals would agree more favorably if waters of comparable hardness had been used for the fathead and *Daphnia* chronic tests.

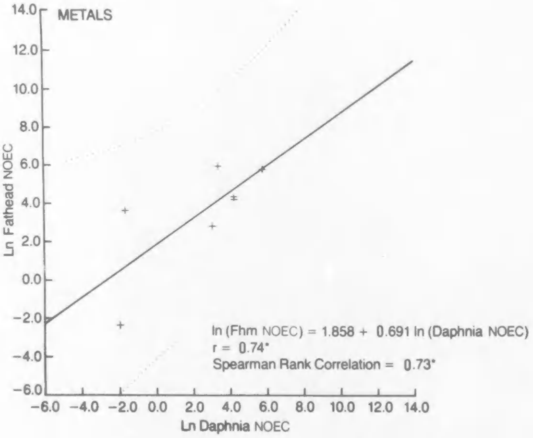


FIG. 3. Linear regression of no observed effect concentrations (NOEC) from chronic *Daphnia* and fathead minnow toxicity tests with seven metals. *$P \leq 0.05$.

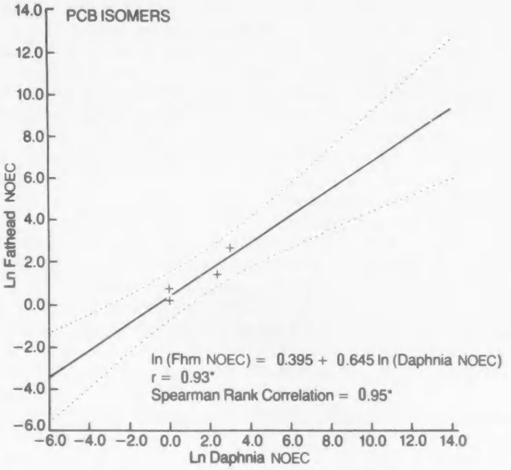


FIG. 4. Linear regression of no observed effect concentrations (NOEC) from chronic *Daphnia* and fathead minnow toxicity tests with four PCB isomers. $^{*}P \leq 0.05$.

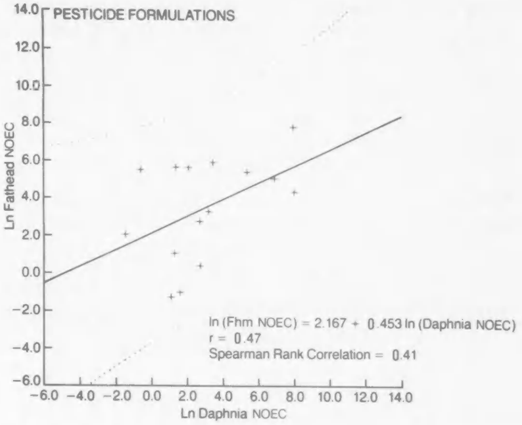


FIG. 5. Linear regression of no observed effect concentrations (NOEC) from chronic *Daphnia* and fathead minnow toxicity tests with 15 pesticide formulations.

PCB ISOMERS

Comparable chronic toxicity data for four PCB isomers (Table 7) all performed at the USEPA Duluth laboratory, were both significant (Fig. 4). The NOEC values for fathead minnows represent estimates made from critical life stage, egg–fry exposures done under continuous-flow conditions. The relatively high *Daphnia* NOEC values reported for PCB 1242 and 1260 represent results from static exposures while the remaining were done under continuous-flow conditions. The higher values reported under static conditions probably reflect reduced nominal concentrations of test material due to settling or glassware absorption under these static conditions. If comparable test data done under intermittent-flow conditions were available for the two species, it is reasonable to expect an even higher degree of correlation between NOEC values for these species.

PESTICIDES

Available chronic data for 15 separate pesticide formulations, the majority of which were tested in soft well water of ~45 mg/L $CaCO_3$ hardness, indicate a relatively poor correlation ($P \leq 0.10$) between fathead minnow and *Daphnia* data (Fig. 5). The extremely wide confidence intervals for the regression equation indicate the high degree of scatter for these values. Since the majority of these tests were done in the same dilution water, toxicity differences due to variable water quality are largely ruled out. It is reasonable to assume that the relatively high degree of variability between pesticide data for these two species reflects the difference in physiology and metabolic pathways affected by these toxicants. Since many of these pesticides were formulated selectively for insect control while creating minimal effects on nontarget species, the more toxic nature of these materials to the invertebrate *Daphnia* is to be expected. Although good comparisons between fathead minnow and *Daphnia* chronic data are shown for some pesticide formulations, it appears that the specificity of mode of action of the pesticide and the difference in physiology between these two test species precludes reliable predictions of chronic fish toxicity from *Daphnia* test data for pesticide formulations.

COMBINED DATA

When chronic toxicity data for all materials summarized in Tables 6 and 7 are combined into a single regression analysis, a comparison evolves for eight detergent components, seven metals, four PCB isomers, 15 pesticides, and the single halogen, chlorine. The combined regressions were significantly correlated (Fig. 6). This relatively good correlation between overall fathead minnow and *Daphnia* NOEC values indicates that the short term *Daphnia* test has significant predictive value for longer term fish toxicity data.

The development of chronic fish toxicity data currently represents a major obstacle for research personnel attempting to determine the relative hazard to aquatic life associated with the use of a new compound. If the cost and time commitment necessary to derive an estimate of a chronically safe concentration to a fish population (i.e. NOEC value) can be significantly reduced through use of predictive correlations employing *Daphnia* as a representative of a lower aquatic trophic level, then it may be possible to develop chronic data for a wider variety of compounds for which previous chronic data was economically unjustifiable based

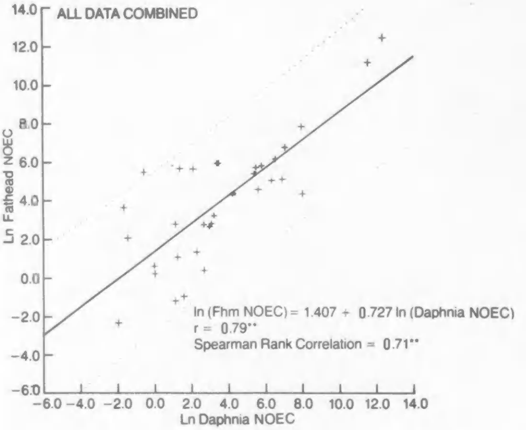


FIG. 6. Combined linear regression of no observed effect concentrations (NOEC) from chronic *Daphnia* and fathead minnow toxicity tests with all 35 test materials. $**P \leq 0.01$.

on low interest or low usage level. *Daphnia magna* offers a short-term alternative test species with predictive value for the establishment of chronic effect data for freshwater fish species. The relatively short life cycle and 21-d duration of the test, small water volumes, ease in handling, and high fecundity make *Daphnia* tests an attractive alternative to the conduct of longer term chronic fish tests.

The correlation between *Daphnia* and fish toxicity values also serves to demonstrate that aquatic safety data developed for the protection of one trophic level may similarly extend to include representatives of a higher level. Before any further position can be developed, it is now important to examine the extent of this correlation with other general classes of compounds and effluents potentially reaching surface waters.

Acknowledgments

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World Distribution of Atlantic Salmon, *Salmo salar*

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Since the mid-19th century, numerous attempts have been made to restore or enhance populations of the Atlantic salmon, *Salmo salar*, within the endemic range, and to establish the species in other parts of the world. Despite all efforts, salmon have become naturalized locally only in eastern North America, Argentina, the Faeroe Islands, and New Zealand. Principal factors affecting the disappearance, restoration, or naturalization of populations are water temperature and availability of suitable spawning and nursery sites. Commercial exploitation of the species in coastal and offshore waters is viewed internationally as a factor of increased importance in the numerical regulation of river spawning runs. A further expansion of the world distribution of Atlantic salmon by naturalization seems unlikely except in areas where preliminary plantings have been made or brood stocks are presently held. Atlantic salmon produced by commercial sea farming operations in Norway, Scotland, Spain, and France are considered to be of comparable quality to fish harvested from the wild. Also, there is presently interest in the potential of sea ranching of Atlantic salmon.

Key words: zoogeography, endemic range, naturalized range, artificial propagation, environmental impact, exploitation, aquaculture

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On a tenté à plusieurs reprises, depuis le milieu du XIX^{e} siècle, de restaurer ou de mettre en valeur les populations de saumons atlantiques, *Salmo salar*, dans leur aire endémique et d'établir l'espèce dans d'autres parties du monde. Malgré tous les efforts, le saumon ne s'est établi localement que dans l'est de l'Amérique du Nord, en Argentine, aux îles Féroé et en Nouvelle-Zélande. Les principaux facteurs affectant la disparition, le rétablissement ou la naturalisation des populations sont la température de l'eau et la disponibilité de sites convenables pour la fraie et l'alevinage. À l'échelle internationale on considère l'exploitation commerciale de l'espèce dans les eaux côtières et en haute mer comme un facteur d'importance accrue dans le controle numérique des remontées de fraie en rivière. Il est peu probable qu'une plus grande expansion de la distribution mondiale du saumon atlantique par naturalisation soit possible, sauf dans des régions où des peuplement préliminaires ont été effectués et là où l'on maintient présentement des stocks reproducteurs. Les saumons atlantiques produits par des piscicultures marines commerciales en Norvège, Écosse, Espagne et France sont considérés comme ayant une qualité comparable aux poissons récoltés à l'état sauvage. En outre, le potentiel de l'élevage en ranch de mer suscite présentement de l'intérêt.

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CONCERN over the future of the Atlantic salmon, *Salmo salar*, had become pronounced by the mid-19th century. Since that time, numerous attempts have been made to restore or enhance populations in waters lying within its native range, and to establish naturalized populations in various parts of the world.

This species was named *Salmo salar* by Linnaeus (1758) and later established as the type of the family Salmonidae. Various other scientific names have since been proposed for salmon frequenting diverse sea- and freshwater environments. These include *S. nobilis* in Iceland (Olafsen 1774), *S. gracilis* for a race in the British Isles (Couch 1865), and *S. brevipes* in the White Sea (Smitt 1882). In addition, unfamiliarity with the life history of anadromous salmon prompted such names as *S. salmulus* for parr (Turton 1807), *S. hamatus* for old males (Cuvier 1829), *S. immaculatus* for young fish from the Strait of Belle Isle (Storer 1850), and *S. argenteus* for kelt in Britain (Günther 1866). In North America, however, the sea-run Atlantic salmon was always considered conspecific with the European *S. salar*, although local peculiarities were sometimes noted (King 1866; Johnson 1901; Kendall 1935; Dymond 1963; Behnke 1965).

The principal names proposed for nonanadromous freshwater (relic) salmon in Eurasia were *Trutta salar relicta* in Lake Ladoga, Russia (Malmgren 1863) and *S. hardinii* in Lake Vänern, Sweden (Günther 1866). Similar fish elsewhere in Scandinavia, such as the "blege" of Lake Byglandsfjord (Dahl 1927) and the "småblank" of the River Namsen (Berg 1953), have

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become recognized as dwarf or relic salmon although once thought to be a form of trout. Also, *Salar obtusirostris* (Heckel 1851), occurring in the rivers of Dalmatia, Yugoslavia, has often wrongly been included under freshwater *Salmo salar* (Regan 1920; Muus and Dahlstrom 1971), or as a subspecies of *S. trutta* (Tourist Association of Yugoslavia 1964), but is, more likely, a separate species of the genus *Salmothymus* (Behnke 1965; European Inland Fisheries Advisory Commission 1971).

In North America, lake salmon were recognized in Lake St. John, Quebec, as early as 1647 (Quen 1648), and later given the common name "ouananiche" (McCarthy 1894a, b) and subspecific recognition as *Salmo salar ouananiche* (Jordan and Evermann 1896). This name has been applied to other populations in Quebec, Labrador, and insular Newfoundland (Chambers 1896; Millais 1907). Lake salmon occurring in the Maritime provinces and the state of Maine were designated as either *S. sebago* (Girard 1854) or *S. gloveri* (Girard 1856; Gilpin 1866).

Despite the observed variability in appearance and ecology that has been noted among Atlantic salmon populations, and the number of scientific names assigned accordingly, it is generally agreed that such differences do not warrant taxonomic distinction even at the subspecific level (Wilder 1947; Nyman 1966; Gray and McKenzie 1970; Westman 1970; Legendre 1973).

The objectives of this paper are to document known attempts to introduce the Atlantic salmon beyond its endemic range and to ascertain the present native and naturalized world distribution. Origin of stocks is given wherever possible. Evidence is presented to identify natural and man-related conditions that affect the welfare of local populations and would seem to limit the establishment of selfsustaining populations of the species.

Native Range

The anadromous (sea) salmon was indigenous to North America in streams along the Atlantic coast northward from the Hudson River drainage in New York state (41°N) to outer Ungava Bay in Quebec (Fig. 1). The species was likely scarce in the Hudson River within historical time, although Robert Juet observed many salmon in the river in 1609 (New York Historical Society 1841b; Edsall 1882), and Hudson recorded that young fish were caught in seines (De Laet 1625 in New York Historical Society 1841a; Rostland 1953). Stragglers entered the river until the early 1800s (Mitchill 1815; DeKay 1842).

North of the Hudson River, nearly every suitable coastal stream within the New England states, Maritime provinces, Quebec, and insular Newfoundland supported a run of salmon (Nettle 1857; Schmitt 1904; Palmer 1928; Kendall 1935; Livingstone 1951; Hawkins, Smith, personal communications). Runs occurred in most of the north shore tributaries of the St. Lawrence River to the Ottawa River, which they may have ascended at least as far as the Salmon River near Montebello (Small 1883), and in south shore tributaries as far upriver as the lower reaches of the Oswegatchie River (Nettle 1857; Smith 1892; Montpetit 1897).

The salmon population in Lake Champlain was considered to be resident (Kendall 1935), but migrant fish could have moved freely between the lake and the St. Lawrence River via the Richelieu River (Watson 1876; Greeley 1929). Spawning runs in the Lake Champlain drainage occurred only in tributaries north of 44°20'N; i.e. to Otter Creek on the east and the Bouquet River on the west shore (Edmunds 1874; Watson 1876). Atlantic salmon were abundant in Lake Ontario where they ascended nearly every tributary (Smith 1892; Parsons 1973). From Lake Ontario, fish were able to run up the Oswego River to Seneca Falls, and sustain populations in lakes Oneida and Cayuga (DeKay 1842; Edmunds 1874), but seldom ascended the large Trent River and were seen only as strays in the Niagara River (King 1866; Fox 1930).

In Labrador, runs occur in all unobstructed rivers with adequate discharge as far north as the Fraser River, Nain Bay (56°40'N lat.). Further north, roving salmon appear in traps set along the coast for Atlantic cod (*Microgadus tomcod*) and Arctic char (*Salvelinus alpinus*) almost up to Cape Chidley (Kendall 1935; Porter, personal communication) and it is possible they approach the coast of southeastern Baffin Island (Power and Cressman 1975). Salmon were known historically to enter Ungava Bay to spawn in the George, Whale (Baleine), and Koksoak rivers (Tuttle 1885; Dymond 1941; Dunbar and Hildebrand 1952; Beck 1962) but may not have been abundant in the nearby Leaf (Feuilles) River until the late 1960s where they were found in appreciable numbers by 1968 (Carter 1968; Jessop et al. 1970). Salmon are taken occasionally along the shore as far northwest as midway between the Leaf and Payne rivers (Power 1969).

There have been verbal reports of Atlantic salmon from the east coast of Hudson Bay north of Richmond Gulf (Hunter 1968). As a cold temperature barrier has prevented movement from Ungava Bay west through the Hudson Strait to Hudson Bay (Low 1896; Kendall 1935; Salonius 1973), it is believed that present, or past, links (e.g. stream capture) between the headwaters of the St. Lawrence and Hudson Bay drainages could have given stray salmon access to Hudson Bay (McAllister 1975), but captures were never confirmed.

Lake or freshwater salmon (sebago) inhabit eastern North American lakes in Maine, New Brunswick, and Nova Scotia along the fringe of the area covered by the Pleistocene glaciation (Power 1958). Original habitats in Maine were the Presumpscot River (Sebago Lake) basin, Sebec River (Sebec Lake) basin, Union River (Reed's Pond or Green Lake) basin, and St. Croix River (Schoodic Lakes) basin (Foster and Atkins 1868; Jordon and Evermann 1902; Havey and Warner 1970); in New Brunswick, the Chamcook lakes and lakes of the upper St. Croix, Magaguadavic, East Musquash (Loch Alva), and Mispec (Loch Lomond) basins (Whitehouse 1948) and the Madawaska near the source of the Saint John River (Adams 1873); and in Nova Scotia, the Grand and connecting lakes on the Shubenacadie River (Whitehouse 1948; Alexander 1975).

Dispersed throughout the more remote areas of Quebec, Labrador, and Newfoundland are numerous populations of lake salmon designated as ouananiche, presumedly differing superficially from the sebago salmon by a smaller ultimate size (Leggett and Power 1969). Distribution extends

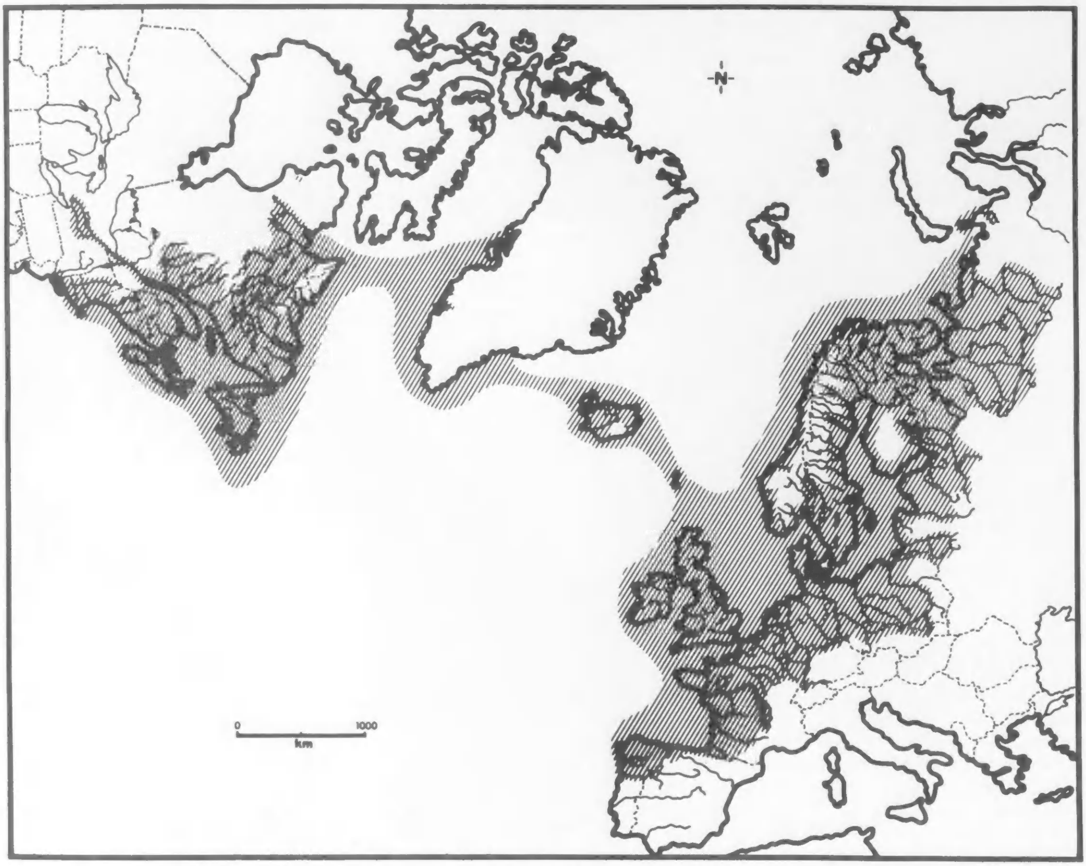

FIG. 1. Historical endemic range of the Atlantic salmon, *Salmo salar*. Distribution in the ocean is approximate.

from the vicinity of the Lake St. John basin on the upper Saguenay River, eastward in the upper reaches of most other rivers flowing from the Labrador Plateau into the Gulf of St. Lawrence as far as the Etamamiou River (McCarthy 1894a; Chambers 1896; Low 1896; Kendall 1935; McAllister 1975; Blais and Legendre 1976). Ouananiche occur also in most lakes of western and central Labrador (Porter, personal communication), and in Ungava Bay tributaries including the upper George River and the Koksoak River drainage between Lake Caniapiscau and Limestone Falls (Low 1896; Power 1958). On insular Newfoundland practically every standing water of 20 ha or larger, and many flowing systems support ouananiche (Scott and Crossman 1964; Porter, personal communication). Although not previously known to occur in waters of the western slope of Labrador that flow to Hudson Bay (Chambers 1896), ouananiche were first recorded from the Kogaluk River of the Hudson Bay drainage (77°18′W; 59°34′N) in 1968, probably the result of a headwater transfer (Le Jeune and Legendre 1968).

From early times the salmon was known to occur in Greenland in the Kapisigdlit River at the head of Godthåb Fjord (Fabricius 1780), but it was not until 1926 that spawning was confirmed with certainty (Jensen 1948). Despite occasional captures, salmon do not naturally occupy other Greenland streams (Nielsen 1961; Jonas, personal communication). In the sea, however, salmon range northward from Kap Farvel to Umanak (71°N) on the west coast and to Angmagssalik (66°N) on the east (Nielsen 1961).

In Europe, the range of the Atlantic salmon extended southward from Iceland, the Barents Sea (Pechora River), and southwestern part of the Kara Sea (Kara River) along the Atlantic coastal drainage to northern Portugal (Douro River) and the Bay of Biscay (Fig. 1). The salmon frequents over 60 rivers in Iceland and is the most abundant in the southwest section (near Reykjavík), numerous in the north, but much less common in the southeast sector because of short glacial rivers containing sea trout, *Salmo trutta* (Gudjonsson personal communication). There is no evidence that salmon spawned in the rivers of the nearby Faeroe Islands (62°N) (Joensen and Tåning 1970; Rimert, personal communication).

Within the British Isles, the salmon was widespread. The larger and more important salmon rivers of Scotland were along the east coast, the west coast rivers being short and arising from lochs. They frequented many of the lochs but never formed a lake population as such (Dawson 1949). Salmon were distributed throughout the Hebridean Islands (Sedgwick, personal communication), but were considered rare in the Shetlands and Orkneys (Dawson 1949). In England, salmon were most abundant in the northeast, from the Scottish border to Yorkshire County; less common along the southeast coast although the Trent and Thames were outstanding salmon rivers; but numerous from the Test and Hampshire Avon near the Isle of Wight, west and north to the Devon Coast and Bristol Channel streams, throughout Wales up to the Border Esk at Solway Firth (Scotland), and on the Isle of Man (Day 1887; Gallichan 1903; Grimble 1913; Dawson 1949). In Ireland, the salmon utilized virtually every river not impaired by low summer water levels or difficult falls at the mouth (Piggins, Went, personal communications).

On the European mainland, the northeastern limit of distribution was, until recent times, the Pechora River and Varandei Island in the western USSR. However, apparently because of a gradual warming trend in the climate from 1919 to 1938, enhanced by a strong inflow of warm Atlantic water, the salmon penetrated eastward into the Kara Sea and was spawning in the Kara River (69°N lat.) as early as 1932 (Jensen 1939; Berg 1948). *Salmo salar* does not occur east of this river, in Siberia, or in the Arctic Islands. Westward from the Kara River, they occur in most rivers of the Barents Sea and White Sea–Murman coast region to the Grense Jakobselv River at the Norwegian border (Berg 1948).

In Norway, more than 100 major rivers and numerous lesser ones along the extensive coast from Finmark County in the north to the Oslo Fjord in the south supported sizeable spawning runs of salmon. Waterfalls were the main limitation to headwater penetration (Berg 1964; Welle-Strand 1971). The west coast rivers of Sweden, flowing to the Kattegat and Skagerrak, also supported runs of Atlantic salmon that had feeding grounds in the North Atlantic (Carlin 1968a; Larsson 1974).

Within the Baltic Sea and connected gulfs, the Baltic salmon originally spawned in some 60 tributary waters in Sweden, Finland, USSR, Poland, and Germany (BRD and DDR). This stock is separated from the Atlantic stock by the Danish Belt Seas with very little overlap between the two populations. Along the Swedish east coast, with exception of the Mörrumsån and a few other rivers in the south, the major salmon rivers were situated in the north from the Dalälven to the Torne älv (Tornionjoki) at the Finnish border (Christensen and Johansson 1975). In Finland the salmon were abundant in tributaries flowing to the Gulf of Bothnia, from the Swedish border to the Isle of Åland. Although salmon were not as numerous, spawning areas extended over most of the rivers in Finland and the USSR in the gulfs of Finland and Riga and in the small rivers of the Baltic coast between the Irves Saurums Strait and Bay of Danzig (Lishev 1959; Hurme 1967; Christensen and Johansson 1975).

Salmon entered the Vistula River basin of Poland as far as the Carpathian Mountains, spawning in headwater tributaries Wisłoka (East Beskids) and Sola and Skawa (West Beskids). They were present in the many small West Pomeranian coast rivers but were never abundant. They ascended the Odra (Oder) River to the headwaters in Moravia (Czechoslovakia) and its main branch, the Warta, to upper reaches of the Welna, Gwela, Plociczna, and Drawa tributaries in Poland (Seeley 1886; Christensen and Johansson 1975; Goryczko, personal communication).

No information exists on former runs of salmon into Baltic tributaries of Germany or the Danish mainland and islands, but most were used regularly by sea trout and considered more favorable for that species (Christensen and Johanssen 1975). Within Denmark's Atlantic Oceân drainage, salmon were present in the River Gudenå (Randers Fjord) on the east coast of Jutland. In West Jutland they ascended the rivers south of the Lim Fjorden but were not present in the Lim Fjorden itself or northern streams (Otterstrøm 1938).

Along the German North Sea coast, salmon ran up the Elbe River to spawning grounds in Bohemia (Czechoslovakia) and Saxony (Germany — DDR), the Weser River system, and the Rhine River system from the Netherlands to the falls of Schaffhausen in Switzerland (Seeley 1886; Hebig, personal communication). They were not known above the falls, in the Boden See (Lake of Constance) or Rhine headwaters (Bruschek, personal communication). In Switzerland, they ascended the major tributary the Aar River up to Thun (Thoune), moving also into Lake Zurich and Lake Wallenstadt by the Limmat and Lake Lucerne by the Reuss (Seeley 1886; Kreitmann 1925). In Germany, they followed the Neckar River tributary at least to Heilbronn, and the Main to Bamberg (Seeley 1886), and the Moselle River to spawning grounds in the Sûre River basin in Luxembourg and in the Vosges mountain region of France (Roule 1920; Koenig, personal communication).

In the Meuse River, which has a common estuary with the Rhine, salmon were abundant throughout the Netherlands and Belgium (Deelder and Drimmelen 1959; Huet, personal communication), and in France up to the region of Charleville and Mezières, and the Semoy, where they spawned (Roule 1920).

Along the northeastern coast of France, salmon occurred principally in the Somme and less commonly in the nearby Bresle, Yères, Basse Risle, and Authie rivers (Roule 1920; Arrignon 1972). They ran up the Seine River to the Cure basin, a tributary of the Yonne, at the Monts du Morvan, where they spawned, and were present in most of the small rivers along the Normandy and Brittany coasts from the Risle River at the Seine estuary to the Blavet and Vilaine rivers in the northwest (Roule 1920).

Further south, major salmon rivers were the Loire, Gironde, and Adour, emptying into the Bay of Biscay. Salmon were found, also, in other smaller streams along this coast but were not as relatively numerous. In the Loire River basin, the majority of the spawners utilized the upper reaches of the Loire and its major tributary the Allier within the Cévennes, Velay, Auvergne, and Forex mountain regions. The remainder ran up the Vienne River branch to spawn in waters of the March and Limousin mountains. The principal spawning grounds in the Gironde River basin existed in the headwaters of the Dordogne River as far as Corrèze, Cantal, and Puy-de-Dôme counties. In the Garonne branch, salmon spawned in the southern region of the Cévennes mountains and at the foot of the central Pyrénées (Roule 1920). The Adour River basin supported runs to spawning areas in the basses Pyrénées at the upper reaches of the tributaries Nive and the Gaves de Pau and d'Oloron. They did not ascend the Adour beyond the junction with the Gaves for purposes of spawning (Roule 1920; Griswold 1926).

In Spain, salmon entered all rivers on the Cantabrian and

Galician coasts from the Bidassoa to the Miño River, shared with Portugal (Gallichan 1904; Borrell 1949; Elegido, personal communication). Salmon entered the rivers of northern Portugal southward to the Douro River (41°N) which they utilized for spawning (Director de Estaçaõ Aquícola, personal communication).

Nonmigratory forms of Atlantic salmon are encountered within the glaciated area of Europe especially in large Fennoscandian oligotrophic lakes (Toivonen 1972). In southern Norway, the "blege" or dwarf salmon occurs in the middle and upper parts of the Otra River basin above the Vigelandsfoss and Hunsfoss and in the upper parts of the nearby Nidelv River (Dahl 1927; Berg, personal communication). In the Namsen River in North-Trøndelag, central Norway, the "småblank" occurs between the Fiskemfoss and the next great falls, the Iofossen and Helvetesfossen, and run up all side rivers and brooks but historically were rarely met with beyond the point where the Storelva River joins the Namsen (Berg 1953).

In Sweden, "blanklax" are present in the Lake Vänern basin where they ascend the rivers Klaraälven (to Østerdal in Norway), Gullspångälven (to Lake Skagen), and Norsälven; and in the Göta River, the outlet of Lake Vänern, above the falls of Trollhättan ("Rudge." 1909; Berg 1953).

Relic salmon (järvilohi) were distributed in Finland in the district of Vuoksi-Saimaa where they occurred throughout the Lake Iso-Saimaa basin, spawning mainly in the Vuoksi River at the outflow of the lake, and the Pielisjoki, which flows from Lake Pielinen at the upper end of the watershed (Seppovaara 1969). They also spawned in the Lieksanjoki, a tributary to Lake Pielinen (Westman, personal communication). In the western Soviet Union, lake salmon occur throughout lakes Ladoga and Onega of the Baltic basin ascending most tributaries to spawn. In the White Sea basin, they are known from lakes Segozero and Vygozero in the Vyg River drainage system, and Lake Kuito in the upper reaches of the Kem' River (Berg 1948).

History of Introduction and Present Distribution: North America

CANADA (TABLE 1)

By the 1860s, salmon had ceased to spawn in all Canadian tributaries of Lake Ontario from Toronto westward, and were rare in streams to the east (Huntsman 1944). On the upper St. Lawrence River above Quebec City, salmon remained plentiful only in the Jacques-Cartier and Ste. Anne tributaries on the north shore and the lower Chaudière River on the south shore, largely due to blockage of natal streams by mill dams (Adamson 1857; Nettle 1857; LeMoine 1863). Even in the Maritime provinces mill dams were interfering with the upriver passage of adult salmon on many rivers (Perley 1850, 1852; MacEachern and MacDonald 1962).

Due to this impending decline, the artificial enhancement of salmon stocks was considered privately for the Jacques-Cartier in 1849 (Nettle 1857), but was not initiated until 1858 when Richard Nettle, Superintendent of Fisheries for Lower Canada, built a small hatchery in Quebec City and hatched eggs of the Jacques-Cartier stock. He continued until at least 1864 (Kirwan 1962; MacCrimmon 1965).

By 1864, Samuel Wilmot of Newcastle, Ontario, had successfully hatched a few hundred naturally spawned Lake Ontario salmon eggs gathered from Wilmot Creek, and the following year, in addition to eggs, also took some adult salmon for stripping (Wilmot 1880b; MacCrimmon 1965). With the creation of the federal Newcastle Hatchery on Lake Ontario in 1868, numerous salmon fry were released into Lake Ontario tributaries and into several inland waters beyond the native range, including Lake Simcoe, Lake Huron, and Lake Erie drainages, and also inland lakes in southeastern Ontario and the Eastern townships of Quebec (Wilmot 1872, 1873, 1877, 1878, 1879, 1880a, 1882). All efforts to establish or reestablish Lake Ontario salmon in these waters were unsuccessful and artificial propagation was discontinued in 1884. After 1898 Lake Ontario salmon were virtually extinct (McCrimmon 1948).

A second effort to introduce the salmon into Ontario waters followed the establishment of a hatchery at Ottawa in 1890 (Veale 1891), with unsuccessful plantings of sea (New Brunswick) and ouananiche (Quebec) salmon in Charleston Lake and lakes of the Ottawa River valley region; in Lake Superior, Georgian Bay, Lake Simcoe, and Lake Ontario drainage basins; and in waters of Algonquin National Park, between 1894 and 1914 (Walker 1895; Prince 1904, 1905, 1906, 1907, 1908; Cunningham 1909, 1910, 1911, Rodd 1913, 1914). Between 1935 and 1963, further intermittent plantings of Lake St. John (Quebec) ouananiche and New Brunswick sea salmon were made in Ontario waters. The suitability of selected Lake Ontario tributaries for smolt production from released fry was confirmed but naturalization did not occur. Only in the Trout Lake system near North Bay was spawning confirmed in 1948 with a selfsustaining population persisting until now (McCrimmon 1948; Whitfield 1948; Gage 1963; MacKay, Wolfe, personal communications). Since 1973, a few Atlantic salmon have been caught in Ontario waters tributary to Lake Huron and Georgian Bay, probably the result of hatchery plantings by the State of Michigan (Loftus, personal communication).

In Quebec, by at least 1868, a private salmon hatchery had been set up on the Moisie River (Whitcher 1871) and continued in operation until about 1918 (Weeks 1971). The federal government established sea salmon hatcheries at Tadousac and Gaspé by 1874 (Wilmot 1880b) and additional hatcheries were completed in later years. Sebago salmon ova from Maine were imported privately and fry released in a water at Portneuf in 1891 and 1892, with some survival up to 1895 (McDonald 1891, 1892; Chambers 1896). Salmon were first introduced to Lake Memphremagog about 1898 and, largely after 1905, to Lake Magog

TABLE 1. History and present status of *Salmo salar* in Canada. fgl, fingerling; yrl, yearling.

Province	First recorded introduction		Known attempts at culture	Annual hatchery production (avg: 1971–75)
	Stock	Year		
Alberta	Sea (N.B.)[a]	1915	to 1923, 1959–63	—
	Lake (Que.)	1918	1918, 1921	—
British Columbia	Sea (N.B.)	1905	to 1934	—
	Lake (Que.)	1918	1918	—
Manitoba	—	None	—	—
New Brunswick	Sea	Native	1868 to present	906 983 fgl, yrl, older
	Lake (Maine)	Native	1880–1971, 1976/77	9 000 yrl (1977)
Newfoundland and Labrador	Sea	Native	Spawning channels	—
	Lake	Native	None	—
Northwest Territories	—	None	—	—
Nova Scotia	Sea	Native	1875 to present	599 406 fgl, yrl, older
	Lake (Maine and N.B.)	Native	1876 to late 1960s	—
	Lake Ontario	1871	1871	—
Ontario	Lake Ontario	Native	1864–84, 1896	—
	Sea (Que. and N.B.)	1876	1876, 1890–1914, 1923, 1938–48	—
	Lake (Que.)	1904	to 1907, 1935, 1949–50, 1952, 1963	—
Prince Edward Island	Sea	Native	1880–1964, 1975	—
Quebec	Sea	Native	1858 to present	922 714 fry, parr, smolt
	Lake	Native	1904 to present	47 186 fry, parr, smolt and adult
	Lake Ontario	1877	to 1880	—
	Lake (Maine)	1891	to 1892	—
Saskatchewan	—	None	—	—
Yukon Territory	—	None	—	—

[a]Origin of stock used by province or state, in initial and future culture; native fish used otherwise.

and other lakes in the Eastern Townships using both sea and ouananiche stocks (Prince 1904, 1905, 1906, 1907, 1908; Cunningham 1909, 1910, 1911).

By the 1950s, sea salmon stocks were present in Lakes Memphremagog, Breeches, Nicolet, and probably Lyster, Lovering, Bowker, Magog, and Massawippi; and ouananiche in Lake Memphremagog and Lac au Sorcier (Maskinonge County) and are known to have been introduced also into Lakes Mégantic, Jacques-Cartier, Tremblant, Archambault, du Cerf, Nominigue, Papin, Papineau, Simon, and Tador (Blais and Legendre 1976; Reardon, personal communication).

Quebec is still endowed with some 50 salmon rivers of major importance although, in the St. Lawrence, few salmon are seen on the north shore above the du Gouffre and the Saguenay. On the south shore, salmon occur upriver only to the Rivière Ouelle. The Mitis (Métis) and Sud-Ouest are the most westernly rivers with appreciable runs (Tétreault 1967; Carter 1968; Reardon, personal communication).

Salmon culture in the Maritimes appears to have begun in 1868 when a private salmon breeding station was built on the Northwest Miramichi River. The salmon eggs procured were sent to United States sources until the fall of 1870 and some hatched for release into the Miramichi River (Atkins 1873). The first government hatcheries to be built in the Maritime provinces were on the Miramichi and Restigouche rivers in New Brunswick in 1873, at Bedford in Nova Scotia in 1875, and on the Dunk River in Prince Edward Island in 1879 (Wilmot 1880b). From these and later hatcheries, salmon eggs and juveniles were distributed into various waters of the Maritime and other provinces.

Salmon stocks reared at Maritime hatcheries have come from a variety of Canadian and United States east coast waters and have been of sea and sebago strains (Atkins 1877, 1880; Prince 1904; Ritter, personal communication).

In New Brunswick and Nova Scotia, no runs of sea salmon have been completely lost but industrial pollution, hydroelectric power development, and pesticide spraying for forest insect control have been responsible for habitat depreciation (MacEachern and MacDonald 1962; Elson et al. 1973; Hooper and Hustins 1973; Needler 1973). The size of runs into some Prince Edward Island rivers has also declined (Smith, personal communication). Some 80% of the present angling catch from the Maritime provinces has been from the Miramichi, Restigouche, and Saint John River systems (Dunfield 1975, 1976, 1977), the Southwest Miramichi River being the highest yielding salmon river in North America with an average catch of 16 450 fish weighing 44 t.

In Nova Scotia, lake salmon populations have declined in some headwater lakes of the Shubenacadie River system, i.e. associated lakes of the Beaver-Rawdon River, due to a combination of factors including increased fishing pressure and destruction of spawning streams (Alexander 1975).

Overall distribution and abundance of salmon on insular Newfoundland and Labrador has changed little within recorded history. Although most populations are continually threatened by overexploitation and industrial development, the salmon would seem to be satisfactorily managed (Porter, personal communication).

The initial transfer of Atlantic salmon to western Canada was a shipment of New Brunswick sea salmon eggs to the Fraser River Hatchery in British Columbia in 1905 (Prince 1905). Juveniles resulting from this and subsequent shipments to this and later the Cowichan Hatchery were planted in selected lakes and rivers on the east coast of Vancouver Island and in the lower Fraser Valley. Ouananiche were being cultured in British Columbia in 1918 (Rodd 1918). The various introductions failed to establish the species in west coast waters although there were some recoveries in the Cowichan River system of Vancouver Island (Rodd 1923; Dymond 1932) with the last known specimen being taken from the lower Cowichan in 1926 (Carl et al. 1959).

Between 1915 and 1923, New Brunswick sea salmon ova were shipped to Banff Hatchery, Alberta, and juveniles released in Minnewanka Lake near Banff and Annette, Edith, Marjorie, Patricia, and Pyramid lakes in the vicinity of Jasper. Also, ouananiche fry were released in Pyramid Lake in 1918 and in Sherbrook Lake (Yoho National Park, British Columbia) in 1918 and 1921. There is no record of any recoveries over the 1915–23 period (Rodd 1915; Kooyman, personal communication).

Between 1959 and 1963, Atlantic salmon were again introduced into National Park waters in western Canada with plantings in the Cascade River, Minnewanka and Cuthead lakes, and Sawback Creek in Banff; Celestine, Moab, and Pyramid lakes in Jasper; and Upper Waterton Lake in Waterton Lakes National Park. No permanent populations were established (Kooyman, Ward, personal communications).

UNITED STATES OF AMERICA

By the mid-1800s, numerous dams prevented sea-run salmon from reaching former spawning areas in all United States rivers along the Atlantic coast, except those in Maine from the Androscoggin north to the St. Croix at the border with New Brunswick (Small 1865; Kendall 1935; Dymond 1963). By that date, salmon were rarely seen in Lake Champlain (Thompson 1853) and, in Lake Ontario, still occurred only in waters at the east end of the lake, notably small runs into the Salmon River (New York Fish Commissioners 1869; Smith 1892).

Within the New England States, government efforts to restore the salmon began in New Hampshire in 1864 with the appointment of fish commissioners. Other states soon followed suit (Atkins 1873). In New York state, Seth Green had privately bought the rights to fishing grounds on the Genesee River, a tributary of Lake Ontario, and built a small hatchery on Spring Creek near Caledonia by 1864. His attempts to transfer salmon ova from Hüningen Hatchery, France, failed because the eggs perished while delayed in customs (Baird 1873; Big Springs Historical Society 1964).

During 1866, Dr Fletcher of Concord, New Hampshire, secured some 25 000 eggs of Miramichi River stock, most of which were placed in artificial beds in the Pemigewassett (Merrimack) River. The remainder were hatched at Concord and Runmey, and released as fry in the Pemigewassett at Compton. A similar operation using a hatchery at Meridith was repeated in the following year (Bellows and Sandborn 1869; Atkins 1873; Baird 1873).

After 1868, salmon eggs of Miramichi stock were shipped to New Hampshire, Massachusetts, New York, Vermont, Connecticut, and Maine under both government and private auspices (Atkins 1873; Baird 1873). Also, in 1870 and 1871 various purchases of Lake Ontario salmon eggs from the Newcastle Hatchery, Ontario, were made by government and individuals in Maine (fry released into the Cobscook and Sheepscot rivers), Connecticut (Houstonic, Farmington, Shetucket, and Quinnebaug rivers), Pennsylvania (the Delaware River watershed beyond the native range), New York (Caledonia Hatchery, Otsego Lake), New Hampshire (Newfound Lake), and Rhode Island (Atkins 1873; Baird 1877; Roosevelt 1884; Meehan 1896; Seamans and Newell 1973). Introductions of Lake Ontario salmon were attempted in Utah in 1873 (Popov and Low 1953), and in Iowa in 1877 (Wilmot 1878).

The first known collections of sea salmon spawn from United States' waters was undertaken in Maine (Penobscot River) in 1871 and 1872. Initial distribution of eggs and fry was made in 1873 in selected waters lying within the native range; in the headwaters of the Delaware, Raritan, and Hudson rivers; in two coastal streams of Long Island; and in the Lakes Erie and Michigan watersheds (Atkins 1873, 1874). By the 1880s, attempts had been made to introduce Penobscot salmon into 14 states beyond the native range (Table 2), but confirmed recoveries were limited to adult fish in Maumee Bay of Lake Erie and the St. Joseph River of Lake Michigan (Jerome 1876).

Along the Atlantic coast there were records, by 1878, of mature adult salmon in every stream as far south as the Susquehanna River in Maryland. However, there was no adequate protection from excessive fishing on these streams and the Holyoke Dam continued to block access to spawning grounds on the Connecticut River (Baird 1879; Hames 1966; Wilde, personal communication). By 1898, construction of dams and severe pollution prevented the passage of salmon on the Merrimack (Bailey 1938), and natural spawning was a failure in the Delaware River (Meehan 1908; Smith 1956). Even on the Penobscot River, the run was maintained largely by artificial propagation (Bowers 1904). By the early 1900s, dams and environmental contamination had made management attempts futile, except in Maine (Table 2).

Culture of lake or sebago salmon was begun in 1866 and 1867 by New Hampshire using New Brunswick St. Croix stocks, with subsequent releases in Newfound, Winnipiseogee, Squam, and Sunapee lakes, and breeding ponds at Meredith (Seamans and Newell 1973). St. Croix (Schoodic Lakes) sebago salmon were first reared by Maine authorities in 1867 and 1868 (Linscott and Locke 1962) and, in 1869 a small hatching-house was built by the states of Maine and Massachusetts on Grand Lake Stream (Atkins 1877). Eggs were sent initially to Massachusetts and Connecticut (Hames 1966; Oatis, personal communication). In following years, rather unsuccessful efforts were made to secure spawn from lake salmon in the Presumpscot (Lake Sebago) and Penobscot (Sebec Lake) drainages (Atkins 1877, 1879; Baird 1877). Stimulated by the success of the Grand Lake project, government or private agencies in 35 states had, by 1907, attempted introduction of lake salmon (Table 2). Other than in Maine, New Hampshire, Vermont, and New York, none of these early efforts met with permanent success.

The first positive response to the demise of the Atlantic salmon along the eastern seaboard of the United States during the early 20th century was by Maine which, in 1948, established the Atlantic Sea Run Salmon Commission. While only the Dennys and Penobscot rivers had small salmon runs by 1926, recent management programs have restored runs in the Penobscot, Narraguagus, Union, Machias, East Machias, Pleasant, and Sheepscot rivers; and sea salmon now inhabit 40% of their native range. Populations are still dependent largely on releases of hatchery-reared smolts (Carter 1975; Rizzo 1975; Belak 1977; Ritter, personal communication). In addition, lake salmon are now resident in over 300 lakes in the state, and about 50% of the populations are self-sustaining (Warner and Havey 1975).

In 1966 Connecticut, Massachusetts, New Hampshire, and Vermont embarked upon a program to restore anadromous fish to the Connecticut River basin, with first plantings in 1967 to the Cold River in New Hampshire (Technical Committee for Fish Management of the Connecticut River Basin 1971). Returns from this and subsequent plantings have been few (Belak 1977; Oatis, personal communication). In 1975, the Pemigewasset River (Mad River tributary) was stocked with salmon (Gulf of St. Lawrence strain) for the first time since the late 1800s (Seamans 1976). Beginning in 1971, releases of Atlantic salmon–brown trout ("sambrown") hybrids have been made by Connecticut into the Farmington River (Connecticut basin) and Latimer and Whitfords tributaries of Long Island Sound (Wilde, personal communication).

The creation of inland lake fisheries for salmon has been a management objective of several eastern states in addition to Maine. In New York state, salmon fishing has been developed in waters in the Adirondacks in such lakes as George, Schroon, Thirteenth, Indian, Eighth, Portaferry; and in Lake Champlain, Cayuga Lake and Neversink Reservoir. Successful spawning is known only from George and Schroon lakes (New York State Department of Environmental Conservation 1977; Neth personal communication). In New Hampshire, where the Lake Winnipesaukee stock is the principal source of eggs, First and Second Connecticut lakes in the north; Lakes Winnipesaukee, Winnisquam, Newfound, Squam, Ossipee, Silver, Dan Hole, Merrymeeting, and Bow in the east central region; and Sunapee and Nubanusit lakes in the southwest are managed for lake salmon (Newell, personal communication).

The stocking of salmon lakes in Vermont was renewed in the 1970s with maintenance stocking of salmon in suitable northern waters, including Harveys, Great and Little Averill, Memphremagog, Seymour, Willoughby lakes and East Long Pond, and feeder streams to Lake Champlain. In southern Vermont, the Chittenden and Harriman Reservoirs have been stocked (Keir, personal communication). Lake salmon from Craig Brook Station, Maine, were introduced into Quabbin Reservoir, Massachusetts, in May 1965 where they first provided angling in 1966 and there is now some evidence of natural spawning in the Swift River (Bridges and Hambly 1971; Oatis, personal communication). The result of 1975 salmon plantings in Laurel Run Reservoir, Pennsylvania, are unknown (Snyder, personal communication). In 1977, the state of Maryland began the incubation of eggs as a first step in an experimental renewal of salmon culture (Woronecki, personal communication).

In the Great Lakes region, introductions of salmon have been renewed by Michigan, Wisconsin, and Minnesota. In 1972, Quebec salmon smolts were planted by Michigan in the Boyne River above Lake Charlevoix, and in the Au Sable River of Lake Huron, and others held at the Wolf Lake Hatchery near Kalamazoo for future brood stock (Michigan Department of Natural Resources 1972). Regular plantings of smolts, largely in the Boyne River, have continued to the present. In 1975 fish of the Swedish Lake Vänern-Gullspång River stock were also planted there. Several hundred Atlantic

TABLE 2. History and present status of *Salmo salar* in the United States of America.

State	First recorded introduction		Known attempts at culture	Avg annual production	
	Stock	Year		State (1971–77)	National (1971–75)
Alabama	—	None	—	—	—
Alaska	—	None	—	—	—
Arizona	—	None	—	—	—
California	Sea[b]	1874	1874, 1890, 1929–32	—	—
	Lake[c]	1877	to 1913	—	—
Colorado	Lake	1881	to 1912	—	—
Connecticut	Sea	Native	1869–1902, 1969 to present	5 345 smolt	35 850
	Lake	1870	to 1914	—	—
	Lake Ontario	1871	to 1872	—	—
	Sambrown[d]	1971	to present	1 456 smolt	—
Delaware	—	None	—	—	—
District of Columbia	Lake	1900	to 1903	—	—
	Sea	1903	1903	—	—
Florida	—	None	—	—	—
Georgia	Lake	(1896)[a]	None	—	—
Hawaii	—	None	—	—	—
Idaho	Lake	1906	to 1931	—	—
Illinois	Sea	1874	to 1875	—	—
	Lake	1876	to 1879	—	—
Indiana	Lake	1878	to 1890	—	—
Iowa	Sea	1875	to 1876	—	—
	Lake	1876	to 1889	—	—
	Lake Ontario	1877	1877	—	—
Kansas	Lake	1879	to 1881	—	—
Kentucky	Lake	1878	to 1881	—	—
Louisiana	Lake	(1885)	None	—	—
Maine	Lake	Native	1867 to present	632 600 fgl, yrl	5 635
	Sea	Native	1870 to present	28 430 fgl, yrl	120 185
	Lake Ontario	1870	to 1871	—	—
Maryland	Sea	1875	to 1901, 1977	—	—
	Lake	1877	to 1894	—	—
Massachusetts	Sea	Native	1868–98, 1968 to present	—	17 790
	Lake	1869	to 1917, 1931–36, 1965 to present	17 240 fgl	—
Michigan	Sea	1873	to 1884, 1972 to present	25 000 smolt	—
	Lake	1876	to 1933, 1973 to present	10 000 smolt	—
Minnesota	Lake	1875	to 1916, 1977	—	—
	Sea	1875	to 1882, 1977	—	—
Mississippi	Lake	1881	None (eggs died)	—	—
Missouri	Lake	1881	to 1882, (1904–05)	—	—
Montana	Lake	1907	to 1937, early 1950s	—	—
Nebraska	Sea	1875	1875 (hatched in Iowa)	—	—
	Lake	1883	to 1885	—	—
Nevada	Lake	1881	to 1892	—	—
New Hampshire	Sea	Native	1866–1904, 1931, 1967 to present	30 000 fgl	416 ('75)
	Lake	1866	to present	136 275 yrl	—
	Lake Ontario	1871	1871	—	—

Table 2 (*Concluded*)

State	First recorded introduction		Known attempts at culture	Avg annual production	
	Stock	Year		State (1971–77)	National (1971–75)
New Jersey	Sea	1873	to 1882	—	—
	Lake	1878	to 1917, 1951–53	—	—
New Mexico	Lake	1959	1959	—	—
New York	Sea	Native	1866–1904, 1910, 1944	22 240 fgl	60 138 ('75)
	Lake Ontario	Native	1871–75, 1877	—	—
	Lake	1876	to present	160 000 fgl	—
North Carolina	Lake	1878	to 1916	—	—
	Sea	1881	1881	—	—
North Dakota	Lake	1905	1905	—	—
Ohio	Sea	1873	to 1875	—	—
	Lake	1876	to 1903	—	—
Oklahoma	—	None	—	—	—
Oregon	Lake	1904	to 1905	—	—
	Sea (Que.)	1951	to present	22 620 fgl, yrl	—
Pennsylvania	Lake Ontario	1871	to 1872	—	—
	Sea	1873	to 1905, 1929–30, 1970–75	—	—
	Lake	1876	to 1898, 1918–24	—	—
Rhode Island	Lake Ontario	1872	1872	—	—
	Sea	Native	1873–90, 1969, 1972–74	—	—
South Carolina	Sea	1902	1902 (Federal plant)	—	—
South Dakota	None	—	—	—	—
Tennessee	Lake	1876	to 1882	—	—
Texas	Sea	1881	None (eggs died)	—	—
Utah	Lake Ontario	1873	to 1875	—	—
	Lake	1899	to 1903, 1924–38	—	—
Vermont	Sea	Native	1869–97, 1931, 1935, 1969 to present	—	—
	Lake	1876	to 1964, 1970s to present	3 334 adult	—
Virginia	Lake	1876	to 1890, 1899	—	—
	Sea	1882	to 1884, 1899	—	—
Washington	Lake	1904	to 1910, 1935	—	—
West Virginia	Lake	1878	to 1881	—	—
Wisconsin	Sea	1873	to 1881, 1972–73, 1977	—	—
	Lake	1875	to 1915	—	—
Wyoming	Lake	1886	to 1911	—	—

[a] Parentheses indicate for exhibition.

[b] Generally stocks from New Brunswick to 1870, then from Maine, unless indicated.

[c] Generally from Maine lakes.

[d] Hybrid, *Salmo salar* × *S. trutta*.

salmon are presently being caught annually by trolling in the open waters of Lake Michigan and in Lake Charlevoix. There have also been captures in or near the Au Sable River in the Lake Huron basin. Mature adults were returning to both the Boyne and Au Sable in good numbers by 1976, but the significance of natural reproduction is not yet obvious (Frankenberger, personal communication).

In Wisconsin, Quebec salmon smolts were released from the Bayfield Hatchery into Pike Creek on Lake Superior in 1972 and 1973, but none returned to the Creek and few fish were caught in the lake (Threinen, personal communication). At present, juveniles of Quebec salmon are held at the Bayfield Hatchery (Addis, Frankenberger, personal communications). To date in Minnesota, Quebec and Gullspång stocks have been hatched at Lanesboro Hatchery, for likely release into some inland waters in the northern part of the state

(Daily, personal communication).

In the western United States, introductions of Atlantic salmon have been limited to Oregon and New Mexico. Releases of the progeny of eggs of Quebec salmon received by the Oregon Game Commission in 1951 and 1958 have been successful only in Hosmer Lake (upper Deschutes basin), where angling is limited to fly fishing with a barbless hook and fish must be returned to the water. A brood stock is maintained at Wizard Falls Hatchery (Oregon Department of Fish and Wildlife 1977; Griggs, Jensen, personal communications). In New Mexico, fingerlings of Maine lake stock were released into Eagle Nest Lake in 1959, but the species has since been replaced by kokanee (*Oncorhynchus nerka*) and coho (*O. kisutch*) salmon (McCleskey, personal communication).

MEXICO

In 1892, 25 000 lake salmon eggs were shipped to the Mexican Fish Commission from the United States (McDonald 1892). There is no indication that the species has become naturalized (Alvarez 1950; Kasuga-Osaka, personal communication).

Europe (Table 3)

BELGIUM

With the building of numerous navigation locks on the Meuse Basin beginning in the 19th century, the salmon gradually disappeared from Belgian waters with the last report of a capture being in 1936 (Huet, personal communication). Lake salmon (sebago) eggs were imported from Maine (USA) both in 1898 and 1901 with no evidence of success (Ravenel 1898, 1901).

CZECHOSLOVAKIA

By 1877, salmon runs were limited by dams and pollution to the Vltava (Moldau), Otava (Wottawa), Orlice (Adler), Divoka Orlice (Wilde Adler), and Kamenice (Kamnitzbach) streams in the headwaters of the River Labe (Elbe) in Bohemia (Hebig, personal communication) where spawning continued until 1928 when the erection of a floodgate at Střekov blocked the passage of fish. Experiments to restore spawning runs through the use of fish ladders proved unsuccessful (Český Rybářský Svaz, personal communication). Salmon were present in Bohemian streams until 1935, and in the Vistula basin of Slovakia until 1959 (Lohniský, personal communication).

CYPRUS

Salmon eggs from Britain (U.K.) were received for experimental culture by the Government Trout Farm at Kalopanayiotis, Troodos Mountains between 1971 and 1973 (Aluastassiades, Demetropoulos, personal communications). Some spawn was collected from the resulting brood stock during 1974–75, but survival was poor. As the species was unsuited to the Cyprus climate, all the hatchery stock was discarded in 1977 (Aluastassiades, Stephanon, personal communications).

DENMARK

Mainland — No more than six rivers in West Jutland presently support salmon runs and appreciable runs occur only in the Storaaen, Skjern, and Varde. As in the Ribe and other rivers with sporadic runs, all populations are endangered by urban development and overfishing (Eskildsen, personal communication). On the east coast, salmon were completely exterminated in the River Gudenå by 1930 with the construction of the Tange Generating Station (Otterstrøm 1938).

Only a few salmon smolts are presently cultivated for live release because of insufficient water and a strong emphasis on farming rainbow trout (*Salmo gairdneri*). Local plantings may at times sustain or establish sparse populations in some rivers (Christensen, Eskildsen, personal communications). The results of releases of smolts into the Laeså and Ølea streams on the Island of Bornholm in 1972 are still to be formulated (Christensen and Johansson 1975).

Faeroes — Salmon are not considered to be native to the Faeroe Islands, but as a result of importations of Icelandic fry by the Faeroe Trout Fishery Society between 1947 and 1957, recoveries began in 1958, one being caught near Selatrađ and another at a depth of 130 m, north of the Faeroes. Mature fish were caught in rivers at Skálabotnur and at Saksun beginning in 1962 (Joensen and Tåning 1970; Rimert, personal communication). From 1963 to the present, regular plants of salmon fry of Iceland and/or Faeroes stock have been made from the Tórshavn Hatchery, which was build in 1962. At present, salmon populations are established near Tórshavn, at Skálabotnur (Fjarđara River), and at Saksun (Rimert, personal communication).

Greenland — Salmon are still selfsustaining in the Kapisigdlit River, but there are indications of a serious decline blamed on an Eskimo fishery at the stream mouth during the spawning season (Jonas, personal communications).

Attempts to establish salmon in eight streams of southwest Greenland (Godthåb and Julianehåb districts) began between 1956 and 1959 with imports of eggs and fry of Canadian (Miramichi) and northern Norwegian (Hammerfest) stock, and the transfer of parr from the Kapisigdlit River (Nielsen 1961; Jonas, personal communication). Despite occasional captures of adult fish, the probability of important natural reproduction occurring in any southwest Greenland stream is doubtful because of inadequate spawning and rearing areas (Jonas, personal communication).

Intensive netting of the Atlantic salmon off the

Table 3. History and present status of *Salmo salar* in Europe.

	First recorded introduction			
Country	Stock	Year	Known attempts at culture	Avg annual hatchery production
Belgium	Sea	Native	none known	—
	Lake (USA)[a]	1898	to 1901	—
Czechoslovakia	Sea	Native	yes	—
Cyprus	Sea (U.K.)	1971	to 1977	stock disposed of
Denmark				
Mainland	Sea	Native	? to present	12 000 smolt
Faeroes	Sea (Iceland)	1947	to present	50 000 fry
Greenland	Sea (Canada, Norway, and Native)	Native	1956–59	—
Finland	Sea	Native	1870s–present	125 000 smolt
	Lake	Native	? to present	43 000 smolt
France Mainland	Sea (Scotland 1970s)	Native	1850s–present	10 000 smolt, 14–21 000 parrs, 85 000 fry
Kerguelen Islands	Sea (Denmark)	1975	to present	unknown
Germany (BRD & DDR)	Sea	Native	experiments 1758, 1772, 1870–1950s, 1966–73	possible experimental plants
	Lake (USA)	1881	to 1891	—
Iceland	Sea	Native	1884–present	130 000 smolt, 46 000 fgl, 55 000 fry
Italy	Sea (Scotland latest)	1885	to 1891, 1928, 1969–71	—
	Lake (USA)	1897	to 1901	—
Ireland (Eire)	Sea	Native	about 1851–present	2 660 000 fry, fgl, smolt
	Lake (Que.)	1908	1908, 1926 (N.B.)	—
Luxembourg	Sea	Native	1891–1949	—
Netherlands	Sea	Native	pre-1882 to ? 1940s	—
Norway	Sea	Native	1853–present	6 200 000 fry, fgl, smolt
	Sea	Native	? to present	8 400 fry
Poland	Sea	Native	about 1869 to present	4 192 smolt, 40 000 fry
Portugal	Sea	Native	after 1925–present	few thousand parr
Spain	Sea	Native	early 1900s–present, greater numbers since 1949	200 000 fry
Sweden	Sea	Native	1860s–present	2 000 000 smolt
	Lake	Native	? to present	under 60 000 smolt
Switzerland	Sea	Native	1857–1947 (experiments pre 1850)	—
U.K.				
England	Sea	Native	1851–present	10 500 smolt quantity of ova and fry
	Lake Ontario	1877	to 1879	—
	Lake (USA)	1883	to 1892	—
Wales	Sea	Native	1926–present	695 000 fry, parr, older; some ova
	Lake (USA)	1902	to 1903	—
Scotland	Sea	Native	1853–present	up to 18–20 million eggs produced
	Lake (USA)	1884	to 1900	—
Northern Ireland	Sea	Native	1881 (?)–present	100 000 smolt, 267 750 fry
USSR	Sea	Native	1852–present	1 400 000 parr and smolt
	Lake	Native	1936–present	fry

[a] Parentheses indicate source of stock first introduced.

Greenland coast began in 1959 near Napassoq after the identification of the Davis Strait as an important feeding ground of migrant European and American spawning stocks. The impact of the Greenland fishery on salmon welfare has been detailed elsewhere (Fraser 1968; Netboy 1968; Lank 1972). Presently, the Greenland territorial salmon fishery has been set an annual quota and the high seas fishery has ended (Department of Agriculture and Fisheries for Scotland 1975; Lank 1976; International Atlantic Salmon Foundation 1978).

FINLAND

By 1900, the impact of dams and electrogenerating plants had caused the extinction of salmon populations in the small southern rivers of Ähtävänjoki, Lapuanjoki, Kyrönjoki , Paimionjoki, and Mustionjoki which formerly grossed an estimated 70 000 smolts per year (Toivonen, Westman, personal communications). By 1931 and 1938, respectively, salmon fishing in the western and eastern arms of the Kymijoki River on the Gulf of Finland had been adversely affected. Construction of a power station at the Pirilä Rapids (Harjavalta) on the Kokemaenjoki in 1940 prevented salmon access to upriver nursery areas (Järvi 1948). By midcentury, salmon had also disappeared from the Uskelanjoki, Aurajoki, and the Eurajoki of southeast Finland because of dams and pollution (Hurme 1967). Similarly in northern Finland, power dam construction on the Oulujoki beginning in 1945 and on the Kemijoki from 1948 eliminated salmon populations by blocking spawning migrations (Järvi 1948; Hurme 1962, 1966, 1969). Salmon ceased to spawn in the Iijoki in 1971, but the stock from this river was saved in fish farms (Westman, personal communication).

Gulf of Bothnia tributaries still supporting salmon runs are the Tornionjoki (at the Swedish border), Simojoki, Kuivaniemenjoki, Kiiminginjoki, Siikajoki, Pyhäjoki, Kalajoki, and Lestijoki (Toivonen, personal communication). In southwestern Finland, near the Isle of Åland, a few salmon still migrate into the Halikonjoki and, as well, the Kiskonjoki as far as the Latakartano Mill rapids (Hurme 1967). Out of the former large salmon rivers, only the Tornionjoki and Simojoki are without power stations; but, in the latter river, channelization of rapids for timber transport has decreased salmon numbers (Westman, personal communication).

Relic or landlocked Baltic salmon in the Lake Iso-Saimaa basin have, since the end of the 19th century, suffered drastically as a result of timbering, domestic pollution, and dam construction and, with the impairment of such spawning streams as the Pielisjoki and Lieksanjoki, are sustained by smolt plantings. Commercial fishing in Lake Iso-Saimaa is no longer profitable (Seppovaara 1969; Hurme, Toivonen, Westman, personal communications).

As a result of dams, pollution, water regulation and timber transport, the present annual production in Finnish rivers is estimated at 435 000 smolts or 22% of the original number (Toivonen, personal communication). No river restoration programmes are underway; however, salmon stocks are held in Government Fish Culture stations and smolts released annually (Hurme, Westman, personal communications).

FRANCE

Mainland — Salmon were abundant in many rivers of France at least until the late 18th and mid-19th centuries when exploitation of the fishery was increased by new markets made accessible by the advent of rail transport (Kreitman 1940). Also, the needs of the salmon were ignored in the harnessing of hydroelectric energy. Returning salmon were cut off from pristine spawning grounds on the upper Garonne River, the Dordogne River, the Vienne River (Loire basin), and the Gave de Pau (Adour basin) (Boisset and Vibert 1945). Industrial and urban pollution became an effective barrier to migration (Roule 1933) and there was apathy towards fishery regulations (Boisset and Vibert 1945). This situation worsened in the early 20th century (Roule 1920, 1925, 1933). By 1966, only 2400 ha of suitable spawning ground remained in all of France despite considerable effort to restore runs by artificial propagation. Only in the Adour basin was it successful (Bouisset 1928; Boyer 1930; Kreitman 1940; Netboy 1968). Various attempts at introduction of lake salmon from the United States began in 1881 when eggs from Grand Lake Stream Station, Maine, were sent to the Société d'Acclimation. From this lot, 2000 fry were hatched and placed in Lake Chauvette in Auvergne (Baird 1881). Culture attempts continued up to 1887–88 (Mather 1887; McDonald 1888). Results of these introductions were not indicated and there was apparently no further culture of Maine salmon. In 1931 eggs of "blege" were imported from Norway for experimental culture. Further importations were considered in an attempt to acclimatize the "blege" in Pyrénée lakes but details are lacking (Jammes and Pénic 1931). There are no landlocked salmon populations in France at present (Chimits, personal communication).

Beginning in 1964, the Conseil Superior de la Pêche moved to increase salmon stocks in various water systems in northwestern France, with priority going to the Bresle, Yères, Basse Risle, and Authie rivers. Initial plantings with eggs of Scottish stock from the Polly River, using Vibert incubators, were concentrated on the Bresle River in 1965 and 1966. From 1968 to 1971, salmon eggs were again obtained from Scotland, hatched at the Piscicultures Gamache, Vouga or Paraclet, and released as alevins or parr. By 1972, adult salmon had become at least as abundant as sea trout in the Bresle. Plans are now being made for a hatchery with a minimum production of 50 000 smolts (Arrignon 1972).

In 1969, the Association pour la Protection et la

Production du Saumon en Bretagne et Basse-Normandie (APPSB) was formed and began studies on the Norman–Breton rivers. Salmon fry of Scottish stock have been released in the Scorff River since 1973 (66–100 000 per year). Plans for a Centre Salmonicole, with a production capacity of 150 000 smolts annually, are formulated (APPSB 1972, 1975). In addition, a management and restocking program was initiated on the Aulne and Elorne rivers (Finistère) and Scottish salmon planted in small tributaries of the rivers in 1974. The first return of salmon occurred in the Elorn in 1976 (APPSB 1977; Harache personal communication). Recoveries of salmon planted in the Nivelle River near the Spanish border, beginning in 1971, began in the 1976–77 season (Davaine, personal communication). Sea culture of Atlantic salmon in coastal waters of Brittany is being investigated (Harache, personal communication).

At present, salmon runs in the Pyrénéean Gaves of the Adour River and the Allier River of the Loire are the main sources of natural recruitment. Runs occur also in streams along the Norman–Breton coast of which the Sélune, Sée, and Orne (Normandy) and the Blavet, Ellé, and Aulne (Brittany) have appreciable runs. Migrant fish in the Nivelle are limited to the lower reaches by an impass at Olha. Overall, today's production of salmon in France is considered insignificant to earlier times (Netboy 1968; APPSB 1972; Davaine, personal communication).

Kerguelen Islands (49°S) — In 1975, 50 000 Atlantic salmon ova of Danish domestic stock were imported and, while the balance of the fry obtained were held at the hatchery, 9000 were released in four lakes. The hatchery water was, however, too cold for successful rearing of salmon and after 1 yr only 1000 fish remained. These were put in the lakes that had been previously stocked. The fate of the planted salmon is not yet determined (Davaine, personal communication).

GERMANY

Salmon began to disappear from many German rivers around 1860, especially in the Rhine and Main basins, because of rapid industrialization along these water courses bringing with it dams and pollution. After 1890, catches decreased catastrophically in both of the latter rivers (Klausewitz, personal communication). On the Elbe basin, by 1890, salmon only frequented the Lachsbach in Saxony. The species is now absent from rivers of the Federal Republic of Germany (BRD) and the German Democratic Republic (DDR), although net catches along the Baltic Sea coast confirm that fish still frequent Polish tributaries of the Oder River (Hebig, personal communication).

Following Jacobi's experiments with salmonid culture at Nortelem as early as 1758, and other successful experiments at establishments on the River Weser, in the Palatinate of the Rhine, and high mountain regions of Germany by 1772 (Haime 1873; Milner 1873), practical salmon culture in Germany began in 1870, when inland fishermen hatched and released juvenile specimens into local rivers (Klausewitz, personal communication). After 1871, over 500 000 salmon ova were hatched annually at the Huningen Hatchery for stocking the waters of the Rhine. This hatchery was established in 1850 by French authorities but came under German jurisdiction in 1871 (Armistead 1895). The Lachsbach Hatchery began releasing 120 000 salmon annually into various brooks of Saxony in 1886 (Hebig, personal communication). Between 1881 and 1891, over 300 000 eggs of Schoodic salmon from Maine were shipped to the Deutsche Fisherei-Verein (Atkins 1881, 1882; Mather 1883, 1885, 1886; McDonald 1887, 1888, 1889, 1891). Some eggs were shipped to Freiburg and Huningen hatcheries for experiments and fry were initially planted in deep mountain lakes in Bavaria (Behr 1882). From these and later releases, the salmon reportedly survived well in Wurm and Tegern lakes (southern Bavaria), in waters near Oliva (Prüssia), and in a pond near Friedrichshuld in Pomerania (Borne 1885). It was decided after 1891 that the American stock offered no advantage over sea salmon, and importations were discontinued.

A remarkable increase in salmon catches, correlated with the plantings, ended abruptly in the late 1880s. Thereafter, the cost of salmon culture was not deemed to be justified economically and propagation had ceased before the end of the century. Several further attempts made in the 20th century failed because of river pollution (Klausewitz, personal communication), and there have been no adult recoveries of 12 000 smolts stocked in two small Kiel Bay streams (western Baltic) between 1966 and 1973 (Christensen and Johansson 1975).

ICELAND

The present health of salmon stocks in Iceland may be attributed to effective management. Before World War II, the species was declared a "freshwater fish" with netting in estuaries and saltwater forbidden, and strict fishing rules implemented. Also, a program of stream improvement was initiated that included the building of fish passes such as that built in 1937 at the foss on the Fitjá River, a tributary of the Vídidalsá, adding 40.2 km of good spawning water (Netboy 1968; Gudjonsson 1969). By 1969, fish passes had opened up over 200 km of previously inaccessible river areas for spawning and nursery grounds. Further, the regulation of water flow in salmon rivers has resulted in improved fishing quality (Gudjonsson 1969).

Culture was begun in 1884 (Gudjonsson 1967) and, from 1886 to 1890, artificial breeding was carried out on the Laxá i Kjos and Laxá i Dolum (Netboy 1968). The life of many small hatcheries built over the next 50 yr was limited by a difficulty in securing salmon eggs. However, the Elliđaar Hatchery, owned by the

Reykjavik Hydro Electric Company, has operated continuously since 1932 with a capacity of one million eggs (Gudjonsson 1967). Transfer of adult salmon has been useful, also, in increasing salmon production. In the Flókå, for example, which was originally barren of salmon, the release of ripe adults from other rivers about 1944 resulted in natural spawning and the creation of a resident stock by 1949 (Stewart 1951).

Since 1961, more rearing stations have been constructed and there are presently some 15 salmon hatcheries in Iceland with smolt releases beginning in the 1960s. At the Kollafjördur Hatchery, heated water has been used to speed up the hatch of salmon eggs to gain a longer growing season in the 1st yr (Gudjonsson 1969; Alexandersdottir, Isaksson, Gudjonsson, personal communications).

IRELAND (EIRE)

Appreciable salmon runs still occur in all rivers that supported pristine populations, except in the Avoca River (County Wicklow) where almost extinction of the species has been a consequence of drainage from old mine workings (Piggins, Went, personal communications).

The implementation of management techniques dates back to 1851 when the range of salmon in the Ballisodare River (County Sligo) was extended above a falls at tideway by the transfer of three pairs of salmon and some ova from the River Moy to the Owenberg tributary. Juvenile survivors were observed in 1853. With construction of a fish pass at the Lower Falls in 1852 (the first successful large fishpass to be built in Europe), a second pass at Collooney on the Owenmore tributary in 1853, and a third at the Upper Falls in 1855, salmon were free to ascend to the upper waters for the first time; and by 1858, the river had become well supplied with salmon (Went 1940). Similarly, a fish pass was installed in the Ennistymon River (County Clare) in 1963 which opened up 43.5 km of new habitat above the head of tide (Netboy 1968).

Culture of salmon was initiated in 1852 on Lough Corrib (Galway). By 1856 about 20 000 young salmon were being held there annually (Anonymous 1856; Nettle 1857). Introductions of Canadian lake stocks were made in 1908 with ouananiche from the Ottawa Hatchery, Ontario, to Ballynastragh, Gorey (Wexford County) (Cunningham 1909); and in 1926, with sebago salmon from the Chamcook lakes, New Brunswick, to various Irish waters (Rodd 1926). Between 1960 and 1970, experimental work was carried out on the production and rearing of salmon and sea trout hybrids (Piggins 1970). At present around 2.5 million sea salmon fry, fingerling, and smolts are released into natural waters from Irish fish hatcheries (Went, personal communication).

ITALY

Atlantic salmon are not native to Italian waters. Known, but unsuccessful, attempts at introduction were made in the Ticino River, a tributary of the Po in northern Italy, in 1885; and in the Lago di Patria, located near Napoli (Naples), in 1891 (Sommani, personal communication). In 1897, eggs of lake salmon were shipped to the Royal Geographical Society, Rome, from the United States. Later shipments were made to Rome in 1898, to Milan in 1901, and to the Misa and Metauro rivers, tributaries of the Adriatic Sea, in 1928 (Ravenel 1897, 1898, 1901; Sommani, personal communication).

Between 1969 and 1971, fry hatched from Scottish salmon eggs were released in the Magra River in Tuscany, a tributary of the Tyrrhenian Sea, at an altitude of about 500 m where annual water temperatures range between 5 and 18°C. Growth was good, with survivors seemingly migrating to the sea at 1½ yr old. Although it was rumoured that some 1-kg grilse similar in appearance to lake brown trout were caught in the Magra River in 1974, there have been no confirmed returns of adult salmon to date (Sommani, personal communication).

LUXEMBOURG

A decline in salmon numbers in the Sûre basin of the Rhine system began in the 1930s despite the release of thousands of fry annually between 1891 and 1942. Further releases of fry between 1946 and 1949 seemed to revive the fishery, but the hatchery closed in 1950 because of difficulty in securing eggs. The last salmon captured from Luxembourg waters was reported in 1956 (Koenig, personal communication).

NETHERLANDS

Rapid industrialization, especially in the first half of the 20th century, led to the demise of the Atlantic salmon in the Netherlands. Principal factors were navigational channels, drainage schemes, pollution, and eventually hydroelectric dams. Also, weirs built on the Rhine and Meuse rivers from about 1925 made it practically impossible for migrating fish to reach their natural spawning grounds. The Dutch salmon fishery completely died out during the 1950s (Deelder and Drimmelen 1959; Drimmelen, personal communication).

From at least 1882, likely before, the Netherlands Government aided in the planting of salmon fry in the Rhine basin by subsidizing large private hatcheries with total plantings, from 1882 to 1892, of over 7 million fingerlings and nearly 160 000 yearlings (Hoek and Bourguin 1893). Some culture of Rhine salmon may have continued until the 1940s, but this is unconfirmed.

NORWAY

Norwegian rivers still sustain sizable salmon stocks and, in some instances, runs have increased. Only on the south coast has fishing deteriorated in recent years owing to pollution, power stations, and salmon nets (Welle-Strand 1971). The lowering of pH by air pollution is of concern in these waters as this phenomenon has already affected relic salmon stocks in the Otra and Nidelv river systems of southern Norway (Berg, Vasshaug, personal communications).

In northern Norway, a moderating climate since 1900 has allowed salmon to ascend several rivers because of glacier retreats (Berg 1964). However, the salmon run on the Pasvikelv River (Kirkenes, Varanger fjord) is now terminated at the Russian power station at Boris Gleb, a distance of only 3.5 km up river (Welle-Strand 1971).

The use of salmon ladders to extend the use of nursery areas above waterfalls was begun as early as 1873 on the Gaula River (Bygstad, Sunn fjord) and, at present, at least 250 are in operation. Some 1000 km of new river stretches have become accessible to sea salmon since World War II (Welle-Strand 1971; Berg, personal communication).

Salmon culture was first attempted in 1853 and 1854 at Lierelven, near Drammen, southern Norway, with first plantings of fry in the Lierelven River in 1855 (Vasshaug, personal communication). Also, an early attempt to raise sea salmon to maturity in freshwater was made in Lier in 1857 (Prince 1900a). First releases in northern Norway were sometime before 1864 (Berg 1964).

The saltwater culture of salmon to marketable size began at Engervannet near Sandvika (Oslo fjord) and Hunedebunnen in Østfold in 1869 using enclosed saltwater pools. In 1872, a third saltwater rearing station was built at the upper end of a sea loch near Larvik and, about 1875, a smaller unit in Fjellskilen on Sotra Island (near Bergen). Survival was inadequate to yield a profit, and all units were eventually dismantled (Jensen 1963). In 1961 the company A/S Mowi became interested in farming Atlantic salmon and, after pilot experiments, commercial fish farming was begun. Smolt rearing stations were established at Øyerhamn on the island of Varaldsøy in Hardanger fjord and at Tveitevågen, Askøy. A sea enclosure was completed at Flogøykjølpo near Møvik on the island of Sotra in 1969 and a larger unit at Veløykjølpo by 1970. Today this enterprise near Bergen has a yearly production of around 500 t (Edwards 1976). There are at least four other fish stations in operation rearing salmon for the domestic market (Vasshaug, personal communication).

Between 1967 and 1973, Norwegian hatcheries have produced annually about 5.8 million fry, 206 000 one-summer-old fingerlings, and 210 000 smolts of sea salmon, and some 8400 relic salmon fry for live release. Most of the hatcheries in Norway are private, upheld by local sport fisheries and subsidized by the government (Central Bureau of Statistics of Norway 1971, 1973, 1974; Vasshaug, personal communication).

POLAND

A small stock of salmon still spawns in the Drawa River, with sporadic appearances of the species in other rivers. Salmon were abundant in the Odra (Oder) River basin until the beginning of severe water pollution in the 19th century. By the early 1900s, annual catches had decreased to about 150 fish (Chrzan 1947). With development of Silesian industry about 100 yr ago, salmon in upriver waters became restricted to the Drawa and Gwda rivers where natural conditions for spawning have been preserved, but the population is now considered to be endangered (Chrzan, Goryczko, Sych, personal communications).

In the Vistula River basin, salmon were still caught commercially up to 50 yr ago. Subsequent water pollution and construction of dams and power stations blocked access to spawning grounds in the lower tributaries, such as the Søla and Skawa, and the numbers of salmon gradually diminished. Annual catches never exceeded 1 t after 1945. The construction of an electropower dam at Włocławek, on the middle Vistula, completely barred migrating salmon from entering the upper reaches after 1968 and, at present, salmon are seldom caught in the lower Vistula (Chrzan, Goryczko, Sych, personal communications).

In the Pomeranian rivers of northern Poland (between Firth of Szczecin and Gulf of Gdańsk), salmon were never abundant but a decrease in numbers was noted after 1945. The catch of salmon in these rivers is, presently, less than 1% of that of the sea trout (Chełkowski 1965; Goryczko, Sych, personal communications).

Attempts at culture and planting of Atlantic salmon within the region of present-day Poland had been undertaken by 1869 or 1870 when the Odra River was first stocked. By 1879, it had received about 1.5 million fry of unknown origin (Kaj 1953). More recent releases have included plants of salmon smolts, from stock imported from Sweden, Lithuania, and Estonia, into the Vistula River and a tributary, the Brda, between 1924 and 1926 (Kulmatycki 1931); Swedish salmon smolts into the Brda River from 1934 to 1937 (Kulmatycki 1940); and Indalsälven River smolts (Sweden) into the Dunajec, a Vistula tributary, in 1962 and 1963 (Żarnecki 1964).

A large breeding station was built at Jazwiny on the Drawa River in 1972 but, so far, has experienced difficulty in rearing smolts. A small number of fish are held in ponds as brood stock to supplement eggs collected from natural spawners. Hatchery-reared smolts are released annually into the Drawa River (Bartel, Chełkowski, Sych, personal communications). Recently, the Rega River (West Pomerania) was stocked experimentally with Drawa River fry (Christensen and Johansson 1975; Sych, personal communication).

PORTUGAL

In Portugal, only the Minho (Miño) River maintains a small salmon spawning run, although few stragglers still enter the Lima and Cávado rivers each year and fish are taken sporadically in the lower Douro River and the Coa and Sousa tributaries (Director da Estação Aquícola, personal communication).

Salmon were abundant in northern Portuguese rivers until the late 18th and early 19th centuries, but began to decrease in most rivers in the late 1800s because of the effects of river hydraulic works and harbor improvements at the river mouths. Another factor was the development of intensive export fisheries, which, by the 1930s, permitted few adults to reach the breeding areas (Alfaro-Cardoso 1931; Machado 1935; Director da Estação Aquícola, personal communication).

Releases of salmon were begun about 1925 and have been continued intermittently to the present, but, because of a difficulty in getting eggs, plantings have been small and of questionable value. The results of plantings of parr in the Minho and Lima rivers beginning in 1972 are, as yet, inconclusive (Director da Estação Aquícolo, personal communication).

SPAIN

Atlantic salmon presently enter only the north and northwest rivers of the Provinces of Galicia, Asturias, Santander, and Guipuzcoa (Basque region), between the Miño to the south and the Bidassoa to the east. Fish from five northern rivers flowing into the Bay of Biscay, the Sella, Deva-Cares, Pas, Narcea, and Asón, accounted for some 72% of the total Spanish salmon catch in 1974 (Roch-Carulla, personal communication). No salmon have been taken for a great many years from the Spanish section of the Duero (Douro) River basin (Caubet-Iturbe, Rueda-Ramos, personal communications).

During the 19th and early 20th centuries, salmon disappeared from many Spanish rivers. Overnetting had destroyed the fisheries in the Sil, Miño, and presumedly other rivers by about 1900 (Gallichan 1904). Construction of mills and hydroelectric dams, removal of water for irrigation, lack of enforcement of fisheries legislation, and divided government jurisdiction for maritime and river fishing, all contributed to the general decline of the salmon. By 1930, only some 20 000 salmon (91 t) were being taken annually, and stocks were further depressed by a lack of harvest controls during the Civil War (1936–42). Following the end of the Civil War, a law was passed to ban all nets in salmon rivers and their estuaries, and fishing legislation again enforced. This action was followed by a modest program of rehabilitation utilizing restocking, fish ladders, and the removal of unnecessary obstructions to migration (Netboy 1968).

Releases of salmon fry into Spanish rivers date back to the beginning of this century, but substantial numbers of salmon (200 000 fry annually) have been planted only since 1949 (Elegido, personal communication). Since 1974, there has been interest in the mariculture of both Pacific (*O. kisutch*) and Atlantic salmon. Atlantic salmon of Icelandic and Norwegian stocks have been reared at a private hatchery on the Río Landro, near Vivero, since 1976 with first transfers to nearby sea cages in late 1976 and early 1977. At least two other companies are hoping to include Atlantic salmon in commercial sea farming operations (Harache 1977).

Present threats to the salmon resource include dangers of overfishing by professional rod fishermen and the construction of dams, such as those built on the Lérez River at Celulosas in 1964, the Ulla River at Portodemouros in 1968, and the Miño River at Creciente (Frieira dam) in 1970, thus limiting the stretches of water available to ascending sea salmon that reach weights to 18 kg (Garcia-Borregon, personal communication).

SWEDEN

Salmon runs now occur chiefly in central and northern Baltic rivers flowing into the Gulf and Bay of Bothnia. West coast salmon rivers, tributary to the Kattegat and Skagerrak, have been badly damaged by dams and pollution and, consequently, only the rivers Örekilsälven, Göta älv, Ätran and its tributary the Högvadsån, Lagan, and Stensån have noteworthy smolt production (Carlin 1968a, Larsson 1974). The once important Lake Vänern fishery has been reduced to annual harvests of only a few tonnes as an effect of hydroelectric power stations and pollution from the pulp and paper industry (Grimås et al. 1972). It was during the 1940 decade that new hydroelectric development made a severe impact on the big northern rivers (Montén 1959). Natural smolt production, estimated at 4 million annually at the turn of the century, had dropped to 1.6 million by 1970 (Lindroth 1974).

While the artificial propagation of salmon was begun as early as the 1860s with annual plantings of a few million unfed alevins in salmon rivers, it was not until about 1930 that fry were retained in ponds for autumn release. By 1950, some 1 million parr and 6 million fry were planted annually. Plantings made in inaccessible areas above dams or unsuccessful fish passes extended the use of several streams for smolt production. However, dissatisfaction over the status of salmon stocks led, in 1946, to creation of the Migratory Fish Committee (now Salmon Research Institute) by the

State Power Board and Fisheries Board, and steps were taken to rear salmon to the smolt stage. First smolt releases were made about 1951, with annual plantings averaging nearly 2.1 million smolts since 1972 (Lindroth 1963; Johansson, personal communication). The smolts migrate to the sea after stocking and return as adults to the river of origin with nearly perfect homing ability. Contribution from Swedish rivers accounts for at least two thirds of the total salmon stock in the Baltic, yielding an average catch return of about 455 kg of salmon per 1000 smolts released (Carlin 1968a, b). In Lake Vänern, a restocking program, especially using the Gullspangsälven strain, has shown good prospects (Grimås et al. 1972).

SWITZERLAND

Salmon have disappeared rather recently from the High-Rhine basin of Switzerland, although the decline in abundance began with the building of many hydroelectric dams on the Rhine and the Aar rivers between 1898 and 1920 with generally inefficient fish passes, if any (Vibert 1949). Construction of a power station at Kembs on the lower Rhine by 1933 effectively blocked upriver migrations but, when the dam was destroyed about 1944, there was some revival of the fishery in the upper Rhine until increasing pollution in the 1950s made conditions impossible for the salmon. The last fish were caught in Swiss waters in 1958 (Office Fédéral de la Protection de l'Environment, personal communication).

Attempts at culture and live release took place before the middle of the 19th century, but details are not recorded until 1857 when young salmon, reared from Rhine River stock at the Huningue Hatchery, were introduced into the Bay of Noville of Lac Léman (Lake of Geneva). Further plantings were made in 1860 and 1863 to Lac Léman and in 1869 to the Orbe, a tributary of Lac de Joux (Chavannes 1869). Regular plantings in Swiss waters of salmon fry, likely of Rhine River stock, continued from 1875 to 1932 with annual releases averaging 1.3 million fish. After the Kembs power station commenced operation, inadequate parent fish were available for spawn taking by the 1940s but, with destruction of the dam, sufficient adults again moved upriver to provide brood stock. Releases of some young salmon were made in 1946 and 1947. The hatchery program was then discontinued (Office Fédéral de la Protection de l'Environment, personal communication).

UNITED KINGDOM

England and Wales — Salmon were plentiful throughout England and Wales until the onset of the Industrial Revolution in the late 18th century. Thereafter, fisheries were neglected, reaching their lowest ebb by 1860 because of excessive net fishing in the estuaries, poaching in the upper reaches, construction of dams with improper or no fish passes, and industrial and domestic pollution (Seeley 1886; Grimble 1913). Salmon fisheries of the Thames declined after 1794 and were virtually extinct by 1820 although a few salmon entered the polluted estuary as late as 1864 (Day 1887).

In Wales, the introduction of grinding machinery in the lead mining industry early in the 19th century had, by about 1860, doomed the salmon runs in the Ymymym, a tributary of the Dovey, the Ystwyth and Rheidol rivers, and other streams on the north shore of the Bristol Channel and the bays of Swansea and Carmarthen. In addition, rivers of Wales were hard fished, poached, and partially blocked by weirs (Gallichan 1903; Grimble 1913; Jones and Howells 1969).

Efforts at salmon restoration by culture and release procedures began in England in 1851 when spawn was collected from Tees River stock and placed in a prepared gravel bed in a tributary of the Swale (Yorkshire). Young fish were noted in March 1852 (Anon. 1853). In 1861 Frank Buckland successfully incubated salmon eggs, obtained in Lancashire County, in hatching boxes. Beginning in 1862, several attempts were made by Buckland and others to restock the Thames and, for several years, thousands of fry were released at Sunbury and Molesey, but without success. Despite the removal of weirs and stake-nets and erection of fish passes, plantings of salmon fry in the Stour from 1866 were also unsuccessful because of pollution (Fitter 1959). A hatchery was started at Milton Abbey on the Frome (Dorsetshire) in 1867 and another by the Duke of Northumberland in 1868, an example quickly followed by other landowners (Grimble 1913).

Salmon ova for these private hatcheries were procured from diverse sources. From 1877 to 1879, a total of 100 000 salmon ova from Lake Ontario stock were sent to Lord Exeter, F. Buckland, and J. C. Cassel (Wilmot 1878, 1879, 1880a) with unspecified results. Maine lake and some sea salmon eggs were shipped to fish-culture associations and private individuals in England between 1883 and 1892 (Mather 1883, 1885, 1886; McDonald 1891, 1892). A consignment of "sebago" eggs was sent to Upper Downing, North Wales, in 1902 and 1903 (Titcomb 1902, 1903). The earliest culture of sea salmon in Wales, however, was not until 1926 on the Afon Conway (Ayton, personal communication).

Despite continuing releases of juveniles, salmon had almost disappeared from the Norfolk coast by the 1880s. By 1902 streams that drained nearly one sixth of the total area of England and Wales, in particular the Bristol Avon, Thames, Mersey, Calder, Weaver, Taff, Loughor, Neath, and Ebbw, were "absolutely denuded" of fish solely by sewage, mining, and factory pollutions (Grimble 1913). Such rivers as the Wye recovered because of the associated action of riparian owners, while rivers like the Tyne, Wear, Tees, and

Trent, continued to yield only a few hundred netted salmon each per year (Dawson 1949). The likely annual harvest of salmon by rod and net fishermen from all the principal English and Welsh rivers seldom exceeded 50 000 fish after 1930 (Netboy 1975).

In Wales, a declining lead mining industry in Cardiganshire by the beginning of the present century had allowed a slow recovery of the rivers, but it was not until 1952 that the reappearance of salmon in the Rheidol River was confirmed. Thereafter, the recolonization of this river was assisted by restocking projects initiated in 1953, the installation of a fish lock on the hydroelectric dam, and a fish ladder at Rheidol Falls which opened up a previously inaccessible stretch of river as far as Gyfarllwyd Falls (Jones and Howells 1969).

In 1968 the Usk River Division put forward a plan to improve water quality in the Ebbw Rawr system. An effluent treatment plant was functional by 1973, but residual pollutants within the spawning gravel still impair natural breeding. Prospects of fisheries based on natural recruitment in coalfield rivers such as the Ebbw Fawr are still slight (Turnpenny and Williams 1977).

Present problems of concern to salmon managers in England and Wales are salmon disease (ulcerative dermal necrosis) and river quality as there is still a sparcity of salmon runs along the east and southeast coast of England between the Humber Strait and the Isle of Wight, and a continuing reduction in abundance elsewhere. Improvement in water quality is an objective of the various water authorities (Maitland 1972; Liddell 1973). The first known capture of an Atlantic salmon in 140 yr from the Thames River occurred in 1974 at the West Thurrock power station (Netboy 1975), while no less than 14 salmon were taken from the improved Trent River in 1974–75 (Tinker 1976). At least three more salmon have been found in the Thames, the latest in April of 1978 (Anonymous 1978).

The Water Authorities, along with the Ministry of Agriculture, Fisheries and Food, undertake the live release of some salmon smolts but facilities for production are limited. The Welsh National Development Authority distributed 26 500 smolts in 1975–76 from a smolt-rearing station at Llanfrynach (Ayton; Ministry of Agriculture, Fisheries and Food, personal communications). The experimental rearing of smolts in barren Welsh mountain tarns such as Llynau Dyrnogydd, Teyrn, and Cilan has resulted in high survivals to smoltification, but use of this procedure as an alternative to conventional hatchery systems requires further study (Sinha and Evans 1969; Harris 1973).

Scotland — Beginning in the late 18th century, salmon became adversely affected by increased industrialization at a time when the increasing value of salmon was stimulating greater exploitation, especially by the use of stake-nets in various Scottish firths. Acts were passed in 1862 and 1868 to conserve the fishery, but stake- and bag-nets could still be placed too near the mouths of rivers (Day 1887). By 1877 the lowland rivers and several others in Perthshire, Forfarshire, and Aberdeenshire had become polluted by industrial wastes, particularly in the Tweed system, various tributaries of the Tay and Forth, and the South Esk below Brechin. West coast rivers, like the Leven, Clyde, Irvine, Ayr, Doon, Garnock, and Nith at Dumfries, were greatly injured by sewage and mill refuse (Young 1877). The salmon also suffered from mill dams, fishing weirs, and poaching (Day 1887).

Scottish salmon culture began as early as 1836 when eggs taken from a pair of salmon were hatched by John Shaw in a stream feeding his pond on the Nith River and the fish held for up to 2 yr in ponds (Herbert 1849; Haime 1873; Milner 1873). In 1853, the Stormontfield salmon ponds were built on the Tay River and 300 000 ova were incubated in 300 boxes fixed on a slope beside the river (Anon. 1856; Nettle 1857; Young 1877). The Duke of Sutherland began planting salmon ova in rivers of Sutherland County about 1866 and, within the next few years, had laid down nearly a million eggs (Fitter 1959). Scottish salmon culture began on a large scale following the construction of the Howietoun Hatchery in 1869 (Day 1887).

Lake salmon (sebago) from the United States were shipped to Scotland between 1884 and 1888 (Mather 1884, 1885; McDonald 1888); and, in 1900, 10 000 Quebec ouananiche ova were sent from the Bedford Hatchery, Nova Scotia, to the Strathcona Estate at Glencoe (Prince 1900b). The surviving fry were released in at least three lakes, of which one may have been Loch Uisg on Mull where sebago were said to be present in 1892 (Harvie-Brown and Buckley 1892). At present there is no evidence of the presence of lake salmon in Scottish lochs (Sedgwick, personal communication).

Since the enactment of appropriate protective (1951) and pollution (1961) legislation, there has been an upward trend in salmon catches from Scottish Rivers explained by pollution abatement, reduction of poaching, and removal of the majority of the weirs (Netboy 1968; Mills 1973). Also, in hydroelectric schemes, fishery requirements must be recognized and the loss of feeding and spawning ground compensated by the production and release of hatchery-reared fish (Menzies 1967). At present, salmon are found in all suitable and accessible Scottish rivers and lochs on both the Mainland and the Islands and there is no apparent danger of salmon stocks disappearing from any waters (Sedgwick, personal communication). However, a recent survey has shown that over 160 km of highly polluted rivers do still exist (Liddell 1973).

Presently, stocking of Atlantic salmon is done generally by the District Salmon Fishery Boards on the larger salmon rivers, and by private owners on the smaller rivers with planting usually of eyed-ova or alevins. About 18–20 million eggs are laid down in a normal year (Department of Agriculture and Fisheries for Scotland, Williamson, personal communications).

The experimental rearing of parr and smolts in lochs was first begun in Loch Kinardochy in 1963 (Pyefinch 1969) with an interest developing in the use of sea lochs for domestic salmon production. A commercial operation, was set up in 1974 in Lochailort in combination with a freshwater hatchery at Invergarry for smolt production. At present, there are at least eight companies involved in cage culture of Atlantic salmon on the Scottish west coast with a combined yield projected at 1000 t by 1979–80. In addition, specialists are producing smolt for sale to mariculturists for growth to market size (Loftas 1976; Smart 1977; Sedgwick, MacKenzie, personal communications).

Northern Ireland — Salmon still run into the numerous rivers of Ulster; only the hydroelectric development on the Erne at Ballyshannon just south of the border affects upriver fisheries. Catches in the Foyle District have shown an upward trend from 1920 with the River Foyle now providing nearly 85% of the catch (Netboy 1975).

When salmon culture began within the present boundaries of Northern Ireland is unknown, but young salmon were released in Lough Ash, in 1881 (Fitter 1959; Vickers, personal communication). The Bush River Hatchery, which was releasing smolts by 1910, is now leased by the government and is producing annually over one million eggs, retaining sufficient to rear 100 000 smolts, and selling the surplus. Juvenile salmon are cultured also at the Foyle Hatchery, Newtownstewart, and the Movanagher Fish Farm (Vickers, personal communication). The Foyle Fisheries Commission releases fry into upriver nursery areas above obstacles preventing access to sea-run adults, or smolts into appropriate rivers. In 1970, Icelandic eggs were secured and, recently, ova have been collected from adults taken by stake-nets, electrofishing, or purchased from agencies in both North and South Ireland (Foyle Fisheries Commission 1971, 1972, 1973, 1974).

UNION OF SOVIET SOCIALIST REPUBLICS (USSR)

Most rivers in the USSR still support sizable runs of salmon though not as abundantly as in former time. Natural smolt production in Baltic rivers had dropped from an estimated 700 000 smolts at the turn of the century to about 204 000 as of 1970 (Christensen and Johansson 1975). Details on present salmon production and harvests in the USSR are not available.

Hydroelectric stations have been built in the north since 1926, somewhat affecting salmon runs, although the construction of fishways is required by law. Fish ladders are operated successfully at the Kegum dam on the Daugava in the Latvian SSR, and on the Tuloma River (built in 1937) on the Kola Peninsula (Zhadin and Gerd 1961; Kozhin 1964). In Lakes Onega and Ladoga, timber removal and domestic pollution have also contributed to diminishing salmon stocks (Ovchynnyk 1963; Grimås et al. 1972).

Plantings of Atlantic salmon began in 1852 with releases of large quantities for acclimatization in Chudskoe Lake (Baltic region). Other known introductions beyond the native range, mainly from Neva River stock were made in Lakes Ertyash (Arctic region) and Pskovskoe (Baltic region) in 1891; in River Kura (Ponto–Caspi–Aral region) in the early 1900s; in a reservoir on River Ufa (Ponto–Caspi–Aral region) in 1909; and in Lake Arakul' (arctic region) in 1914. Occasional captures followed, but the salmon subsequently disappeared from planted waters without reproducing. Lake-form salmon apparently were only planted in 1936 in Lake Turgoiak (arctic region) with negative results (Burmakin 1963).

The culture and release of Atlantic salmon is an important management tool being used to counterbalance natural losses resulting from hydroelectric power stations, navigation and irrigation systems, industrial pollution, and intensive fishing (Ovchynnyk 1963). At present, 15 Atlantic salmon hatcheries are in operation on the Baltic Sea and Kola Peninsula with an annual production of 1.4 million (8–14-g) parr and smolt. Two additional hatcheries are under construction (Hutchens 1977). In Baltic tributaries, recent releases of reared salmon juveniles amount to an estimated 575 000 fish annually (Christensen and Johansson 1975).

South America (Table 4)

ARGENTINA

Lake salmon (salmón encerrado) were first introduced into Argentina from the Grand Lake Stream Station, Maine, in 1904 with the arrival and hatch of eggs at a hatchery at Lago Nahuel Huapí (41°S), situated in the Andes Mountains close to the Chilean boundary. The resulting fry were planted in lagos (lakes) Nahuel Huapí, Traful, Gutiérrez, and Correntosa, or held at the hatchery as eventual brood stock (Tulian 1908). Further ova shipments were received between 1905 and 1910 from the United States at the Alta Gracia (Córdoba Province) and Santa Cruz hatcheries. Waters planted with fry included Lago Argentina, Río Santa Cruz, Río Chico and other local bodies of water. Releases into the Río Santa Cruz included sea salmon from the Denbigh Fishery, North Wales. In 1930 fry obtained in Chile as ova were released in waters of the Nahuel Huapí National Park (Tulian 1908; Marini 1936).

A fisheries station built in 1932 on Arroyo Cascada was, because of poor water conditions, replaced by a new hatchery and rearing station at Bariloche in 1937, built principally for rearing not only Atlantic salmon, but brook (*Salvelinus fontinalis*), brown, and rainbow trout for live release. Eggs from naturalized stocks in the Río Traful and other local streams were used (Thompson 1939). Culture of salmon from established stock has continued at the Centro de Salmonicultura de San Carlos de Bariloche, Río Negro Province, to the present (Lourdes-Balz, Mastrarrigo, personal communications). A recent government program for the development of inland fisheries, mainly to increase the supplies of fish to local communities, includes the Atlantic lake salmon (FAO 1975).

Salmon are selfsustaining in various lakes and rivers of the Argentine Patagonia, notably in ríos Traful, Minero, Collón-Curá, Limay and lagos Traful, Curruhué Grande, Hermoso, Correntoso, Meliquina, Huechulafquen, Lacar, Lolog of Neuquén Province; ríos Ñirihuau, Manso and lagos Moreno, Nahuel Huapí, Guillelmo of Río Negro Province; ríos Chubut, Corcovado, Senguerr and lagos Musters, Colhue Huapí, Fontana, Epuyén, Futalaufquen of Chubut Province; ríos Santa Cruz, Chico and lagos Argentino, Burmestein, Strobel, Cardiel of Santa Cruz Province; and ríos Turbio, Jofré, Ewans, Fuego, Olivia and Lago Fagnana and Laguna Kosobo of Tierra del Fuego (Lourdes-Balz, Mastrarrigo, personal communications).

CHILE

Salmo salar eggs (salmón del Rhin) were first brought to Chile in 1905 from Hamburg, Germany, and hatched at the Estación de Piscicultura de Río Blanco (Golusda 1927). Further introductions continued until 1910 (Mann F. 1954). Fry were distributed in the Aconcagua, Maule, Cautín, and Toltén basins, Laguna del Inca, Calle-Calle and Río Bueno. A small "portable" station was built on the shore of the Río Maullín to facilitate plantings in more southern waters, including ríos Rahue, Maullín, Petrohué and Puelo (Golusda 1927; Eigenmann 1928).

There may have been some initial success but, by the 1950s salmon were considered rare or absent (Mann F. 1954; Buen 1959). At present *S. salar* is not found in Chilean waters, nor is the species cultured (Campos C. 1970; Campo, personal communication).

COLOMBIA

In 1894 3000 freshwater (sebago) salmon eggs were forwarded to Colombia from the United States (United States Commissioner of Fisheries 1894). No records of other shipments were found, nor is the species now present in Colombia (Ramos-Henao, personal communication).

ECUADOR

During the 1888–89 season 5000 salmon eggs were sent from Craig Brook Station, Maine, to New York for transhipment to Quito, Ecuador (McDonald 1888). There are no records of further shipments. The species is not found in Ecuador (Ovchynnyk 1967).

FALKLAND ISLANDS

Attempts at introduction of Atlantic salmon and true sea trout (*S. trutta*) to the Falkland Islands was undertaken from 1960 to 1964. A total of 84 000 salmon and 22 000 sea trout ova from Lancashire County river stock (England) were planted as ova and fry in various rivers in an attempt to establish sea-run stocks. Returning trout migrants were first captured in 1963 but no adult Atlantic salmon were ever taken. There were no other introductions and salmon do not occur in Falkland Islands waters (Stewart 1975).

Africa (Table 4)

SOUTH AFRICA

Despite failures in successfully transferring viable English and Scottish salmon ova to South Africa in 1876, 1889, and 1890 (Day 1932; Hey 1947), Scottish salmon ova were received and hatched in 1896 at the Jonkershoek Hatchery at Stellenbosch, Cape Province. Heavy floods during 1897 washed many of the fry from the hatchery ponds into the Eerste River where they were seen occasionally. A further shipment in 1897 resulted in the release of 5000 smolts in the Dwars (Berg) River in 1898. In that year, the Frontier Acclimatisation Society released 8000 young salmon in a Keiskama River tributary. In both cases the fish migrated to the sea but never returned. A final introduction was attempted in 1906, but the eggs arrived in bad condition at the Jonkershoek Hatchery with only six fish surviving for a short time. There have been no further introductions of Atlantic salmon to South Africa (Inland Fisheries Department 1944).

Asia (Table 4)

INDIA

The first Atlantic salmon ova to reach India were received at the Harwan Hatchery in 1965 but there was no survival beyond the fingerling stage (Wani, personal communication). In 1969 freshwater salmon ova from Craig Brook National Fish Hatchery, Maine, were shipped to Kashmir Province (United States Division of Fish Hatcheries 1969) and the fry reared at Laribal Hatchery (Wani, personal communication). Releases were also apparently made in the feeder streams of high mountain lakes (Bumgarner, personal communication) but there is no indication of survival. The hatchery stock first matured in 1972 but attempts to incubate the ova have been unsuccessful except for a few hundred fry hatched in 1975 (Sreenivasan, Wani, personal communications).

INDONESIA

About 1929, a mixed shipment of rainbow trout, brown trout, and salmon eggs was sent from the Nether-

Table 4. Introductions and present status of Atlantic salmon in South America, Africa, Asia, and Australasia.

	First importation			
Country	Stock	Year	Success	Hatchery production
South America				
Argentina	Lake (USA)[a]	1904	Yes	29 000/year
	Sea (England)	1906	None	—
Chile	Sea (Germany)	1905	to 1950s	—
Colombia	Lake (USA)	1894	None	—
Ecuador	Lake (USA)	1889	None	—
Falkland Islands	Sea (England)	1960	None	—
Africa				
Rep. South Africa	Sea (England)	1876	1896–98, 1906	—
Asia				
India	Sea (?)	1965	to 1966	—
	Lake (USA)	1969	Yes, limited	buildup of brood stock
Indonesia	Sea (Netherlands)	1929	None	—
Japan	Lake (USA)	1895	None	—
Australasia				
Australia				
N.S.W.	Sea (Canada)	1965	Yes, small	buildup of brood stock
Tasmania	Sea (England)	1852	1864–1936 temporarily, each plant	—
Victoria	Sea (England)	1864	1864–80s temporarily, each plant	—
New Zealand	Sea (England)	1864	temporarily, each plant, to 1907; yes 1908 on, small	buildup of brood stock
	Lake (USA)	1905	to 1906	—

[a]Parentheses indicate source of stock first introduced.

lands to Tjobanrondo near Malang. Fry placed in the streams of the Kawi mountain in East Java did not survive (Schuster 1950).

JAPAN

In 1895, the Government of Japan was sent 60 000 eggs of sebago salmon from the United States Fish Commission (Ravenel 1895). There is no further mention of Atlantic salmon, nor is the species included in the list of naturalized species in Japan (Okada 1960).

Australasia (Table 4)

AUSTRALIA

New South Wales — In 1963, the Canadian Government supplied the New South Wales Fish Authority with 100 000 Atlantic salmon ova taken from River Philip stock in Nova Scotia. Fry were hatched at Saw Pit Creek and the survivors moved to Gaden Trout Hatchery where heavy losses occurred. However, 9000 fingerlings were released in Micalong Creek, a tributary of the Goodradigbee River, and a few hundred retained at the hatchery as potential brood stock (François 1963). Additional shipments of 100 000 eggs were received in 1964 and 1965, and further releases of fingerlings made in the same area. Although several adults were caught, there was no evidence of spawning and the population presumedly perished during a long drought and reduced water levels in 1966 to 1968. Small brood stocks are presently carried at Gaden Hatchery, Jindabyne, and Dutton Hatchery, Armidale. Escapees from the Gaden Hatchery are resident in the impounded Lake Jindabyne, although numbers are believed to be small in comparison with other salmonids. Mature salmon are taken occasionally in the Thredbo River, the major spawning stream tributary, but there is no evidence of successful natural reproduction (Tilzey, personal communication).

The future of the species is doubtful because of a lack of midwater food in most coldwater impoundments in the Snow Mountains area, and an apparent inability to compete with brown and rainbow trout. However, releases of hatchery-reared salmon to impoundments will continue (Tilzey, personal communication).

Tasmania — Attempts to introduce salmon into Tasmania from England in 1852, 1860 and 1862 ended in failure. However, in 1864, a shipment of 100 000 salmon ova, collected from Severn, Ribble, Tyne, and Tweed River stocks in England, arrived at Melbourne in good condition. Most of these eggs were sent to Hobart Town, but only 3000 fish were produced. The survivors were released into the River Plenty, a tributary of the Derwent. From a further shipment of

English salmon eggs in 1866, 6000 fry were hatched and planted in the River Plenty during the fall of 1867 (Allport 1870; Wilson 1879; Godby 1927). Fingerlings resulting from further imports of eggs from England and Ireland were liberated in Tasmanian waters in 1884, 1885, and 1888 (Johnston 1888) and in most instances, substantial numbers of smolts descended to the sea (Godby 1927).

Smolts were first taken in the Derwent in 1869, and grilse in 1873. In January of 1876, about 250 fish, intermediate between smolts and grilse, were taken in the open sea off beaches some distance below Hobart Town. In the winter, a pair of adult fish, believed to be salmon, were observed spawning in the Plenty and some eggs taken and hatched (Allport 1878). Positive identification of a small salmon grilse was made in 1877 (Wilson 1879). Despite these encouraging signs, the salmon did not become naturalized.

A much later attempt, in 1909, to establish Atlantic salmon in Great Lake met with failure. The most recent effort to acclimatize the species in Tasmania was in 1936 when ova from a New Zealand stock were imported and 2500 2-yr-old fish liberated in Great Lake. A small spawning run was observed in the Liawenee Canal, a tributary of Great Lake, but the salmon again failed to become established (Lynch 1970, 1973, personal communication).

Victoria — About 3000 ova from the 1864 shipment of English salmon to Tasmania left at Melbourne resulted in the release of 120 fry to the Badger tributary of the Yarra River. There were no recoveries (Wilson 1879). In 1876, a second unsuccessful attempt was made at introduction using English salmon ova in cooperation with the Government of New Zealand. In 1878 about 2000 ova were obtained from a shipment destined for New Zealand and hatched out at Ercildoune. The few survivors were held for a time as potential brood stock (Baird 1878; Wilson 1879).

Additional efforts to introduce salmon into Victoria would seem to have been made, but these are not documented. There is no evidence that salmon have ever been even temporarily resident in Victoria waters (Cavanagh, personal communication).

NEW ZEALAND

The initial introduction of Atlantic salmon to New Zealand was attempted in 1864 with the unsuccessful shipment of 600 young fish from London to Canterbury in tanks (Thomson 1922). Other unsuccessful attempts were made in 1868, 1869, 1871, 1873, and irregularly between 1876 and 1902 with ova of Tay, Severn, and other British stocks. Ova of Rhine River fish were received in 1887. In some instances, some ova survived transport and a few fry were released in waters of both North and South Islands. No planting was successful (Thomson 1922; Stokell 1955; Keillor 1972; Stewart 1975).

North American stock was first introduced in 1905 using eggs of lake salmon from Green Lake Hatchery, Maine. Most of the fry escaped into a race leading to the Makerewa River, and the remainder were placed in Lake Te Anau (Thomson 1922; Stokell 1955). A second undetailed consignment was received in 1906 (Bowers 1906). In 1907, 50 000 eggs of Canadian salmon were received and 11 000 fish released as 2-yr-olds in the Selwyn. Although, in some instances, the young salmon grew freely to the smolt stage and migrated from the rivers, only one recapture, near Oamaru Harbour, in 1896, was positively identified as a sea-run *S. salar* (Thomson 1922; Godby 1925; Griswold 1926; Stokell 1955).

In a final effort to acclimatize the species by intensive stocking, a hatchery was built on the Waiau River near the outlet of Lake Te Anau on South Island. In 1908, 250 000 eggs were obtained from Canada and the fry liberated in a creek flowing into the Upukerora. Both in 1909 and 1911, a million eggs were obtained from British and Rhine River stocks and the offspring planted in the Waiau system. These plantings resulted in establishment of the species in Lake Te Anau and a spawning run in the Upukerora River (Godby 1925; Griswold 1926; Stokell 1955). By 1923, adult salmon were present in plentiful numbers in the Te Anau basin, especially in the Upukerora, Eglinton, and Waiau rivers below Lake Manapouri; and, on one occasion, 650 000 eggs were collected by the Fisheries Department (Calderwood 1927a).

However, the salmon remained resident in freshwater although, between 1916 and 1923, some fish were occasionally caught in or near the sea (Godby 1925; Phillipps 1925). From 1923 until at least 1929, a serious attempt was made to develop a sea-run stock. Several millions of fry hatched from Te Anau eggs were liberated in the Wanganui River in the North Island, but none returned as adults. The overharvest of salmon eggs for this program would seem to have caused a decline of salmon numbers in the Lake Te Anau catchment, first evident in the early 1930s. Although smolts were taken at the mouth of the Waiau River in 1927 and adults reported from the Wairaurhiri River (Calderwood 1927b; Stokell 1955), failure to obtain a large sea-going population caused waning interest in the Atlantic salmon and resulted in substantial releases of rainbow trout (Stokell 1955; Hutchinson, personal communication).

Renewed interest in the Atlantic salmon by the Southland Acclimatisation Society began in 1962 with import of ova from Poland. Also, from 1964 to 1968, the New Zealand Wildlife Service attempted to capture mature wild Te Anau fish to form a brood stock at the Hatchery. As a result, 402 yearling salmon of the latter stock were released into barren Lake Douglas on the west coast in the Southern Alps during October 1966. Subsequent checks have failed to reveal any success (Hutchinson, personal communication).

During 1974 adult salmon were captured in Lake Gunn (Lake Te Anau system) for brood stock and seven were held successfully in a small stream on the Wanaka Hatchery grounds. Chances of holding a brood stock at that hatchery appear good (Hutchinson, personal communication).

In natural waters, the Atlantic salmon is presently confined to the catchments of lakes Te Anau and Manapouri despite efforts at range extension. Numbers remain critically low with small populations surviving in lakes Gunn and Fergus at headwaters of the Eglinton River on the Lake Te Anau catchment. Salmon are caught only occasionally by anglers in the upper reaches of the Waiau River Proper (Graynoth and Skrzynski 1974), and in the more remote portions of Lakes Te Anau and Manapouri (Hutchinson, personal communication).

Discussion

The decline of the Atlantic salmon within its native range during the past 200 yrs, or less, may be identified closely with environmental changes within home rivers, especially the loss of spawning and nursery grounds, resulting from a variety of human activities. Most evident among the cultural impacts are the presence of dams and chemical pollutants that have prevented access of adult fish to former breeding and smolt production areas; and the deterioration of river habitat conditions by various land use practices that have greatly increased siltation and erosion and adversely modified flow patterns and thermal regimes.

Historically, the pristine river habitats within the native range of the Atlantic salmon in both Europe and North America have suffered a similar degradation or demise wherever soil, forest, or mineral resources are capable of sustaining substantial human settlement, or water power may be economically harnessed to serve local or distant social demands. Hence, the greatest environmental damage to salmon resources has occurred in coastal and central Europe, England, the Atlantic seaboard of the United States, and the St. Lawrence and Lake Ontario watershed where, historically, man has extensively exploited land and water resources without due concern for the health of aquatic ecosystems. However, habitats of the Atlantic salmon have not been immune to human impact even in wilderness or sparsely populated areas such as parts of Scandinavia and Finland, Labrador, Quebec, the Maritime provinces of Canada, and the northern New England states, where forest cutting, insecticide spraying, base metal mining, atmospheric pollution, and dam construction have caused temporary or permanent damage to salmon resources (Kendall 1935; MacEachern and MacDonald 1962; Saunders 1969; Elson et al. 1973; Hooper and Hustins 1973; Needler 1973; Yanchinski 1978). The best examples of compatibility between salmon and man occur in Scotland, Ireland, and Iceland where geoclimatic and socioeconomic constraints on human population density and industrial development, plus a commitment for the preservation of salmon and trout rivers, have sustained substantial selfsustaining salmon populations (Menzies 1967; Netboy 1968; Gudjonsson 1969; Mills 1973; Piggins, Went, personal communications).

Water temperature must be considered a principal factor in establishing the native range of the salmon (Dymond 1963). Optimum temperature for egg fertilization and incubation is ~6°C. At early incubation (before eye pigmentation) temperatures below 4°C and above 12°C, normal embryo development is unlikely (Peterson et al. 1977). However, incubation may proceed with water temperature dropping nearly to the freezing point but the rate of development is slow, i.e. 160 d at 1.0°C. At incubation temperatures above 8°C, fungal infections are probable (Power 1969; Havey and Warner 1970; Peterson et al. 1977). Water temperatures of at least 6°C are considered imperative for the growth of juveniles (Peterson et al. 1972), and there is evidence that alevins may not begin feeding below 10°C (François 1963), with spring blooms of microscopic life a necessity at time of hatching (Menzies 1949).

Despite the rather high ultimate upper incipient lethal temperature of 27.8°C (Garside 1973), high seasonal river temperatures, coupled perhaps with other habitat limitations, were undoubtedly paramount in establishing the southern limit of the native range of the Atlantic salmon and, more recently, in causing range reductions where land and water use practices have increased summer maximums in water temperature. As incipient lethal temperatures are determined by acclimation temperatures (i.e. previous thermal history), a sudden increase in ambient temperature of 10°C, or less, may bring about the death of resident salmon at temperatures considerably below the upper incipient lethal. On the other hand, juvenile and adult salmon may live for short periods above the ultimate lethal temperature (Fry 1947), as observed by Huntsman (1942) for grilse in the estuary of the Moser River. McCrimmon (1954) noted that, while exposure to upward diurnal fluctuations in river temperatures killed parr in Duffins Creek after a predictable time lapse, differences in sublethal temperature regimes elsewhere in the stream system had no observed effect on annual survival or distribution patterns. Unquestionably, periodic peaks in river temperatures have been responsible for occasional die-offs of juvenile salmon and, where these occur annually, or in a sequence of years, the presence of selfsustaining salmon populations is impossible. This phenomenon is not necessarily confined to waters near the southern limits of the native or present range.

The final temperature preferendum of 17°C (Javoid and Anderson 1967) indicates the optimum temperature for salmon growth agrees closely with that noted by Linscott and Locke (1962). Even when acclimated as low as 4°C, the selected temperature is 14°C (Fisher and Elson 1950). This would seem to explain the apparent failure of the salmon to move westward through the arctic waters of Hudson Strait and Hudson Bay which reach only 4.5 and 7.0°C, respectively, and has prevented a westward extension of its northern range to the rivers of James Bay and eastern Hudson Bay where habitats and temperature regimes (maxima of 7–12°C) are similar to those in Ungava rivers supporting selfsustaining populations (Vladykov 1934; Salonius 1973).

The other environmental factor that has been instrumental in limiting the native range, or at least distribution within that range, has been the presence of natural waterfalls historically preventing access of migrant adult salmon to rather extensive areas of breeding and nursery grounds. Notable extensions of upriver use for smolt production, especially in mountainous regions of Europe, have resulted in recent years by the construction of fishpasses (Went 1940; Netboy 1968; Gudjonsson 1969; Welle-Strand 1971; Berg, personal communication) and/or releases of hatchery-reared fish or adult transfers (Went 1940; Stewart 1951). Conversely, the construction of many dams has prevented parent salmon from reaching primordial spawning grounds in both Europe and North America. Hence, restoration programs of the future must consider how large areas of presently inaccessible breeding and nursery grounds may be best utilized for smolt production, and how the ultimate movement of smolts to the sea may be best facilitated.

Salmon restoration programs must obviously be concerned with all aspects of stream habitat quality. Dissolved oxygen levels required by salmon ova in redds increase with development and temperature. For example, embryos hatching at 5.0°C need at least 5.8 mg/L (Hayes 1949; Hayes et al. 1951; Wickett 1954). The importance of a stable flow of oxygenated water and abundant microhabitat (gravel–rubble substrate, undercut banks, fallen logs, aquatic vegetation, etc.) for fry survival has been clearly established (Perley 1852; McCrimmon 1954; Havey and Warner 1970; Elson 1975; Symons 1976). Likewise, the need of parr for open riffle sections with adequate depth (15–30 cm), gradient (2.0–11.5 m/km), pH (5.8–7.6), flow (to 90 cm/s) and surface turbulence has been identified (Gibson 1966; Elson 1967; Havey and Warner 1970; Gibson and Power 1975). Too steep a gradient (30 m/km) may limit successful spawning (Mills 1973). Adult salmon are more sensitive to light than juveniles and require deeper water or a canopy to shield them from intensive sunlight (Huntsman 1942, 1965; Gibson 1966). Examination by Huntsman (1944) of streams once occupied abundantly by Lake Ontario salmon revealed that the physical characters of the better streams conformed with the above noted features. McCrimmon (1954) found that the upper reaches of several of these streams, most notably Duffins Creek, to be still capable of substantial smolt production from experimental releases of hatchery-reared fry.

Among those within-stream factors affecting juvenile salmon production, siltation is of prime importance because of its obliterating effect on substrate interstices and other forms of bottom cover to which the fish must relate for survival (McCrimmon 1954). Historically, Edmunds (1874) noted an affinity of Lake Champlain salmon only with conglomerate substrates, not clay bottoms. Although silt has been recognized as a serious stream contaminant in literature dealing with other salmonid species (Shapovalov and Berrian 1939; Bjornn 1969; Hall and Lantz 1969; Hausle and Coble 1976), the importance of silt in suppressing stream production of juvenile Atlantic salmon is but poorly recognized. Turnpenny and Williams (1977), like the authors, stress the polluting effects of silt and note that a stream can be rendered useless for reproduction long after the source of contamination has been removed.

Despite numerous attempts to introduce Atlantic salmon beyond its endemic range, few naturalized stocks have been established. In North America success has been limited to a number of small lakes in eastern Canada and the northeastern United States. These waters are typically deep, cool oligotrophic lakes with feeder streams providing suitable spawning and nursery areas. Lake salmon typically occupy midwater depths just below the thermocline to 20 m in summer, and the upper 4.5 m under ice cover and at other times when surface waters are under 21°C. The species is also naturalized in homothermous lakes which may reach 18–24°C in summer. The salmon surface to feed on insects and, when available, feed heavily on forage species such as smelt (*Osmerus mordax*) resulting in higher production levels (Kendall 1916, 1935; Havey and Warner 1970; Seamans and Newell 1973; Warner and Havey 1975). Present Atlantic salmon stocks in the Great Lakes basin (Frankenberger, personal communication) and in Hosmer Lake, Oregon (Griggs, Jensen, personal communications) are still dependent on releases of hatchery-reared fish.

With the exception of extensions in range to upriver areas previously inaccessible to migrant salmon in Norway, Iceland, and Ireland, the only naturalization of the species in European waters has occurred in the Faeroe Islands (Joensen and Tåning 1970). On other continents, naturalized populations have been established in Argentina along the Argentine Patagonia (Lourdes-Balz, Mastrarrigo, personal communications), and a now endangered stock in the Te Anau basin of New Zealand (Hutchinson, personal communication). Brood stocks are presently held in Kashmir Province, India (Sreenivasan, personal communication) and in New South Wales, Australia (Tilzey, personal communication).

The culture and live release of Atlantic salmon, with the objectives of sustaining, restoring, or naturalizing the species, has a history spanning nearly 200 yr. The well-documented disappearance of the salmon from Lake Ontario during the latter part of the 19th century, despite the release of millions of hatchery-reared fish, was early evidence that no amount of stocking could maintain or restore a fishery in waters that had become environmentally unsuitable (MacCrimmon 1965, 1977). A similar conclusion can be drawn from similar experiences along the Atlantic seaboard and in parts of Europe where extensive culture was undertaken. The lesson is as valid today as then: the stocking of salmon will be ineffective unless integrated with environmental control or enhancement programs. Hence, efforts to reestablish or naturalize salmon populations in unfavorable environments have been a failure. Also, there is evidence from recent studies in the Canadian Maritime provinces that supplemental releases of nonnative stocks into streams may yield lower recoveries of adults than if fish of native parentage are used (Ritter 1975), although this may not always be the case (Jessop 1976).

Various evidences of heritable traits, such as timing of smoltification, age at first spawning, homing, season of reentry, etc., are indicative of the need for a better understanding of relative genetic and environmental influences on survival, growth, and life history patterns of salmon stocks. Appreciation of the "stock concept" may indeed the instrumental in the ability of Swedish hatcheries to sustain the substantial Baltic salmon fishery (Carlin 1968a, 1968b), and, further, may have practical implications not only in the management of wild stocks and the success of attempts at naturalization (Møller 1970), but in recent developments in commercial sea farming (Edwards 1976; Smart 1977) and sea ranching (Thorpe, personal communication).

The significance of exploitation on the welfare of Atlantic salmon resources, and the need for more rigid enforcement of protective legislation, have been controversial international and local issues in recent years (Lank 1972, 1976), and of particular concern to salmon-producing countries with strong lobby from sportfishing organizations. While there is evidence that, in the Lake Ontario drainage for example (Huntsman 1944), overexploitation of river-run adult salmon contributed to local extinctions, it was man-made environmental changes, most notably dam construction, that placed the species in a position of vulnerability to virtual total harvest by legal and illegal means. While the extent of harvest, whether in home waters or on the high seas, is obviously a factor in the numerical regulation of mature salmon returning to home rivers, the actual relationship between potential overexploitation and the degradation of home stream environments requires clarification as a basis for international negotiations on future management of the North Atlantic resource.

In synopsis, it is probable that the present range of the Atlantic salmon can be sustained, and that its endemic range may, at considerable cost, be restored by a rational combination of environmental and resource enhancement coupled with controlled harvests. A further global naturalization of the species beyond locations where either naturalized or hatchery-reared stocks are now present is unlikely. The recently extended role of aquaculture to include sea farming and sea ranching of Atlantic salmon, while not expected to extend the present native or naturalized range of the species, has added a new dimension to the potential of the salmon as a marketable food resource in onshore waters as distinct from traditional commercial and sport fisheries.

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NOTES

A Culture Technique Using Marine Fish Kidney to Obtain Chromosomes

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PARK, E. H., AND S. D. PARK. 1979. A culture technique using marine fish kidney to obtain chromosomes. J. Fish. Res. Board Can. 36: 458–461.

A relatively simple and reliable in vitro method for marine fish chromosome study was developed. The addition of 10% chick embryo extract to serum-supplemented Eagle's minimum essential medium with high concentration of NaCl resulted in marked growth of kidney cells in the marine conger eel (*Astroconger myriaster*) after activation by phytohemagglutinin (PHA). Culture medium without chick embryo extract or PHA and/or with normal concentration of NaCl did not induce substantial growth. In contrast to reports by others, humidified culture was not required for excellent cell growth of these teleost kidney cells. Numerous metaphases unmarred by overlapping chromosomes were recovered and excellent karyograms were available for detailed karyotype analysis.

Key words: kidney, culture, marine fish, chromosome

PARK, E. H., AND S. D. PARK. 1979. A culture technique using marine fish kidney to obtain chromosomes. J. Fish. Res. Board Can. 36: 458–461.

Les auteurs ont mis au point une méthode relativement simple et fiable d'étude in vitro de chromosomes de poissons marins. L'addition d'un extrait à 10% d'embryon de poulet à un milieu essentiel minimal d'Eagle avec supplémentation en sérum et à haute teneur en NaCl produit une croissance marquée des cellules rénales du congre de mer (*Astroconger myriaster*) après activation par phytohémagglutinine (PHA). Un milieu de culture dépourvu d'extrait d'embryon de poulet ou de PHA et/ou avec une concentration normale de NaCl ne provoque pas de croissance substantielle. Contrairement à ce qui a été signalé pas d'autres, on n'a pas eu besoin de culture humidifiée pour obtenir une excellente croissance des cellules rénales de ces téléostéens. Il a été possible de récupérer de nombreuses métaphases non gâtées par chevauchement de chromosomes et on a obtenu d'excellents caryogrammes permettant une analyse détaillée des caryotypes.

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FISHES have received a special importance in recent years not only because of interest in their cytogenetics (Ohno 1974) but also because of their possible use as indicators for the monitoring of environmental carcinogens and teratogens (Pliss and Khudoley 1975; Matsushima and Sugimura 1976). In this connection, the establishment of a reliable tissue culture system for fish cytogenetics was needed.

The most promising cell culture technique from vertebrates is one using leucocytes, because the tedious digestion and centrifugation procedures are not needed. Leucocyte cultures, however, have not enjoyed a great success with fishes compared with homoiothermic animals (Wolf and Quimby 1969; Denton 1973; Blaxhall 1975; Gold 1978). Leucocyte cultures of fishes have succeeded in only limited numbers of freshwater species (Heckman and Brubaker 1970; Legendre 1975; Kang and Park 1975; Etlinger et al. 1976a). Although the phytohemagglutinin (PHA)-culture method using the teleost kidney for obtaining chromosomes developed by Yamamoto and Ojima (1973) as an alternative method to peripheral leukocyte culture assures good results, it has two shortcomings. First, a humidified incubator is needed and second, the technique is not successful with marine fishes. This paper describes a new approach to the study of marine fish chromosomes. This new method, using kidney cells for chromosome analysis, is superior to the alternative one using leukocyte cultures. Furthermore, it eliminates

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the shortcomings mentioned above by the addition of 10% chick embryo extracts in combination with PHA and high concentration of NaCl to the culture medium.

Materials and methods — The culture medium we used was Eagle's minimum essential medium with Hanks salts buffered with N′-2-hydroxyethylpiperazine-N′-ethanesulfonic acid (15 mol/m^3) containing 10% fetal calf serum, 10% chick embryo extract (EE$_{100}$, Difco.), penicillin G (100 IU/mL), streptomycin (100 μg/mL), kanamycin (60 mg/mL), and PHA-M (0.2 mL/10 mL). The concentration of NaCl in the medium was increased from 0.137 mol/dm^3 to 0.2 mol/dm^3. The former concentration represents the one present in mammalian and freshwater fish systems and the latter the one in marine fish serum (Sigel and Beaslly 1973). Initial pH of the medium was adjusted to 7.2 with $NaHCO_3$.

Kidney donors were marine conger eel (*Astroconger myriaster*: Order Anguilliformes) of both sexes. Adult fishes, 40–60 cm long and 400–700 g, were kept in artificial seawater at room temperature. The kidney was aseptically removed after the area behind the portion of the anus where the main kidney is located was cleaned with alcohol. It was placed first in a bath of sterile marine Ca^{++} and Mg^{++} free phosphate buffered saline (M-Ca^{++}, Mg^{++}-F-PBS). The kidney was then transferred to a second bath of M-Ca^{++}, Mg^{++}-F-PBS and then thoroughly rinsed in a third bath of fresh PBS. The tissue was minced with fine scissors without trypsinization. Tissue fragments thus obtained were mixed with fresh PBS. The intertubular cells were liberated and suspended from tissue fragments by gentle stirring with a glass rod. Cell suspension was then allowed to stand for several seconds to remove coarse fragments. By this procedure, a fine cell suspension could be obtained. The upper part of the cell suspension was collected in a conical tube and then centrifuged at 1300 rpm for 8 min. The collected kidney cells were resuspended with the culture medium and were divided into a small tablet bottle (20 mL) containing 10 mL of culture medium. The density of kidney cells was adjusted to 1.5×10^6 viable cells/mL. Cell viability was determined by nigrosin dye exclusion. The culture bottles were tightly stoppered and placed in a dry incubator at 28± 2°C for 3–5 d.

We monitored the effects of chick embryo extracts, PHA, and increased osmolarity on the cell proliferation in cultures by autoradiographic procedures for assessing the DNA synthetic rates. For this purpose, ^{3}H-thymidine (Amersham/Searle) with a specific activity 740 kBq·mol^{-1}·m^{-3} (20 Ci·mol^{-1}·m^{-3}) was added to the cultures at a final concentration of 18.5 kBq·mL^{-1} (0.5 μCi·mL^{-1}) for 1 h before harvesting. After labeling, the radioactive medium was removed and the cells were washed twice with the medium containing 100x concentration of cold thymidine. Following two changes of the fixative (1:3 acetic acid–methanol), the cells were finally resuspended in 1 mL of fresh fixative and then air-dried. The labeled cells were counted with autoradiograms using stripping plate (Kodak AR-10) in the usual manner.

For chromosome preparation proliferating kidney cells were arrested in metaphase by the addition of Colcemid® (0.1 μg/mL) for the final 2 h of incubation, followed by hypotonic treatment with 0.05 mol/dm^3 KCl for 15–20 min. Fixed cells were air-dried and stained with either 10% Giemsa in PBS (6.8 pH) or basic fuchsin.

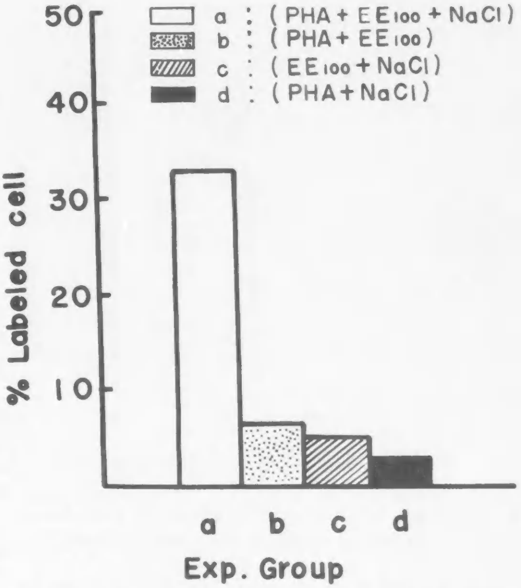

FIG. 1. Labeling indices of cultured kidney cells from marine conger eel in the various culture conditions.

Results and discussion — Renal cells of the marine conger eels in culture showed a typical leukocyte-like growth pattern. The growth rate of the cells in the medium supplemented both with EE$_{100}$ and PHA was remarkably enhanced in high concentration of NaCl (Fig. 1). These results suggest that the 10% chick embryo extract, high concentration of NaCl, and the PHA are important factors in successful cultures of conger eel kidney cells. A large number of metaphases and labeled differentiated cells were observed in this culture condition (Fig. 2 and 3). However, such figures were rare in cultures without supplements.

Although McKenzie and Stephenson (1973) report on the ability of chick embryo extract to improve cell growth in a monolayer culture of freshwater fish cells, the usefulness of the embryo extract has not been tested previously in a marine species. The embryo extract in combination with PHA and high concentration of NaCl was found to greatly promote kidney cell growth of marine conger eels in vitro (Fig. 1).

Kinetic studies showed that maximal proliferation occurred between day 3 and 4 (Fig. 4). Furthermore, humidified culture did not affect the extent of growth. Replicate cultures in a humidified incubator, which had 195 labeled cells, contained only three cells in metaphase out of 2000 randomly scored cells.

Kidney tissue of fishes has been known to have a hematopoietic function (Catton 1951). Thus, kidney cells have a capacity to respond to the lymphocyte mitogens. However, the capacity of mitogens to induce extensive proliferation of lymphocytes from kidney was

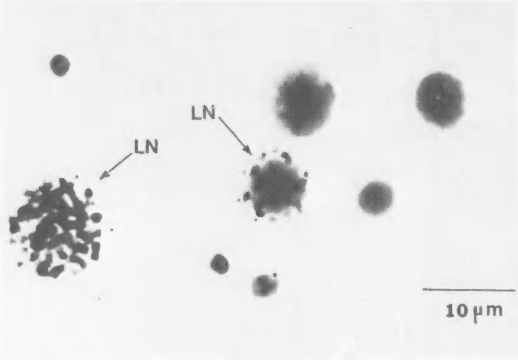

FIG. 2. Autoradiograph showing differentiated cells with grains (LN).

found to be lower than those from peripheral blood in teleost fishes (Etlinger et al. 1976b). This might be one of the reasons why kidney cells of conger eels showed much lower growth in PHA medium without EE_{100} supplement (Fig. 1).

The effect of high concentration of NaCl was examined. The results indicate that conger eels require a high osmolarity for their growth in vitro (Fig. 1). The growth rate was markedly different between 0.2 mol/dm^3 and 0.137 mol/dm^3 NaCl. A higher osmolarity requirement has also been reported for the optimal growth of other marine fish cells in culture (Wolf and Quimby 1969; Li and Clyburne 1977).

There was about 2% of mitosis in log phase in Colcemid®-arrested cultures and a large number of excellent metaphases were available for chromosome analysis (Table 1 and Fig. 3). Karyotypic alterations during the course of cultivation were not detected. Natural karyotype is normally maintained in the present short-term culture compared to our previous direct preparations (Park and Kang 1976).

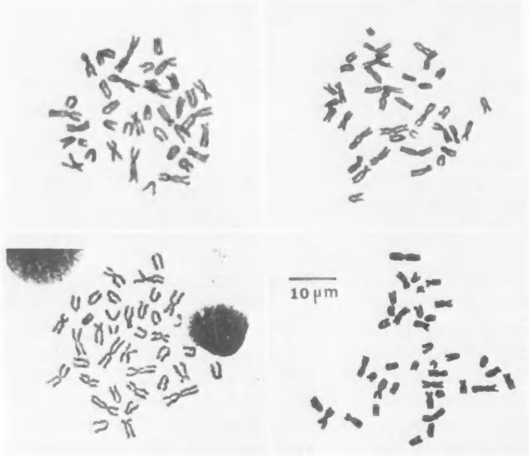

FIG. 3. Metaphases obtained from cultured kidney cells of marine conger eel.

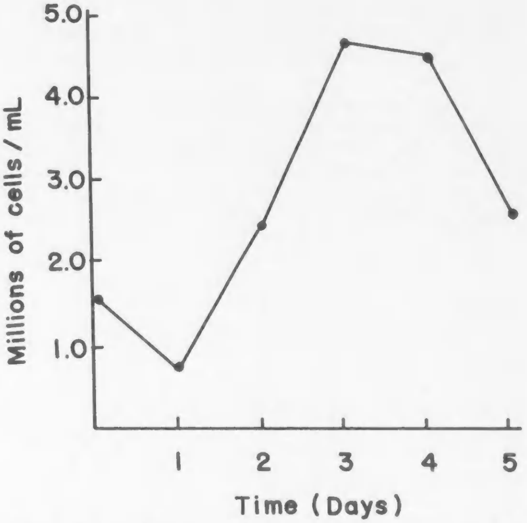

FIG. 4. Growth curve of kidney cells in the complete medium at 28°C.

Incidence of epidermal papilloma in eel and neoplastic transformation in marine fish appear to be closely related to environmental pollution of carcinogenic substances (Peters 1975). Since chromosome aberrations in various animals result from exposure to carcinogens a study of chromosomal alteration of the fish cells exposed to pollutants would be of great interest. Therefore, it is hoped that this culture technique will be useful for studying and screening environmental pollution as well as for researches in the field of marine fish cytogenetics.

Acknowledgments — We are grateful to Dr S. Ohno, City of Hope National Medical Center and Dr J. J.

TABLE 1. Mitotic index[a] of cultured kidney cells from marine conger eel (*Astroconger myriaster*) grown in different culture conditions.

Medium composition[b]			Mitotic index (%)
PHA	EE_{100}	NaCl	
+	+	0.2 M	1.8
+	+	0.137 M	0.1
−	+	0.2 M	0.1
+	−	0.2 M	0.04

[a] Based on scoring of 2000 cells treated with Colcemid® (0.1 µg/mL) for last 2 h and fixed at 72 h after incubation.

[b] Eagle's MEM with Hank's salts and 10% fetal calf serum

Marchalonis, Cell Biology and Biochemistry Section, Basic Research Program of Frederick Cancer Research Center, for their critical reviews of this manuscript.

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In Vitro Maintenance of Amoebocytes from the American Oyster (*Crassostrea virginica*)[1]

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BREWSTER, F., AND B. L. NICHOLSON 1979. In vitro maintenance of amoebocytes from the American oyster (*Crassostrea virginica*). J. Fish. Res. Board Can. 36: 461–467.

Explant and monolayer cell cultures were initiated from oyster heart and embryonic tissue and maintained for periods of a few days to 6 mo depending on the type of tissue and the culture medium. A pH of 7.0–7.3 and a temperature of 20°C were optimum. Vertebrate cell culture media prepared in a marine saline and supplemented with fetal bovine serum and protein digests provided a suitable basal medium. Supplementation of the basal medium with oyster hemolymph or extracts of oyster tissue markedly prolonged cell maintenance. Explant cultures of heart tissue with the subsequent outward migration of individual cells were most easily initiated and maintained for periods up to 6 mo. Although several cell types were observed, actively motile, granular amoebocytes predominated. No mitotic cells were observed

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[1] A summary of this work was presented at the 28th Annual Meeting of the Tissue Culture Association, June 6–9, 1977, New Orleans, La. This work will be presented as part of a dissertation submitted by F.B. in partial fulfillment of the requirements for the M.S. degree from the University of Maine, Orono, Maine.

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even following exposure to a variety of mitogens. Cultures initiated from disaggregated larvae did yield actively dividing cells.

Key words: oyster, cell culture, amoebocytes

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Des cultures d'explants et de cellules en couches uniques ont été amorcées à partir de tissus cardiaque et embryonnaire d'huîtres et maintenues durant des périodes variant de quelques jours à 6 mo, selon le type de tissu et le milieu de culture. Le pH et la température optimaux sont respectivement de 7,0–7,3 et 20°C. Un milieu de culture de base adéquat nous est fourni par des milieux de culture de cellules de vertébrés préparés dans une saline marine et auxquels on ajoute du sérum de fétus de bovin et des produits de disgestion protéique. L'addition au milieu de culture de base d'hémolymphe d'huître ou d'extraits de tissu d'huître prolonge notablement le maintien des cellules. Les cultures d'explants de tissu cardiaque avec migration subséquente vers l'extérieur de cellules individuelles sont le plus facilement amorcées et maintenues durant des périodes allant jusqu'à 6 mo. Nous avons observé plusieurs types de cellules, mais il y avait prédominance d'amoebocytes granulaires activement mobiles. Nous n'avons observé aucune cellule mitotique, même après exposition à divers agents mitogènes. Les cultures commencées avec larves disséquées donnèrent des cellules qui se divisèrent activement.

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THE culture of oyster tissues has previously been attempted by several investigators (Li et al. 1966; Perkins and Menzel 1964; Tripp et al. 1966). Although cultures of viable cells, predominantly amoebocytes, have been maintained for various lengths of time, no cultures of actively dividing cells have been obtained even after exposure to various mitogens (Tripp et al. 1966). Moreover, these studies employed different procedures and various culture media.

The immediate objectives of this study were to develop techniques for the routine initiation of oyster tissue and cell cultures and to optimize conditions for prolonged maintenance of such cultures. Ultimately, such cultures will be evaluated for use in isolating viruses infecting oysters and other molluscs.

Materials and methods — Oysters used in this study were obtained from either Chesapeake Bay or Long Island Sound. All animals were thoroughly scrubbed under a jet of water with a stiff piled brush upon receipt and stored in a humid atmosphere at 4°C in which condition they remained viable for up to 6 wk.

Tissue preparation — Oysters were aseptically opened from the ventral edge and the adductor muscle was carefully severed from the right valve. After removal of the valve, the mantle flap covering the pericardium was retracted, and the area was rinsed with a strong spray of zephiran chloride disinfectant (1:750). Only live animals with the pericardium intact after opening were used. Hearts were removed aseptically and placed into separate sterile test tubes containing 2–3 mL of sterile marine saline (Li et al. 1966) with penicillin G (200U/mL), streptomycin (200 μg/mL) and amphotericin B (5 μg/mL) and maintained at 20°C. The tissues were then washed a minimum of 3 times at 30-min intervals in the above saline.

Larvae were obtained using conditioned adult breeding stocks at the University of Maine's Ira C. Darling Center for Marine Studies in Walpole, Maine. Before spawning, the adults were scrubbed thoroughly with a stiff brush and allowed to rinse for 8 h in running, filtered seawater. Spawning was induced by increased water temperature and the addition of stripped gonad material to the breeding containers. Of necessity, spawning was done under nonsterile conditions, but all further handling of the eggs and embryos was aseptic.

Fertilized eggs were collected on fine mesh (37-μm) nylon screens and rinsed in running sterile seawater for 15 min after being placed in sterile 500-mL beakers. The eggs were then suspended in sterile seawater with added antibiotics (see above antibiotic rinse solution) and maintained at 20°C.

Initiation of in vitro cultures — Prepared tissue was placed in a petri dish with 5–10 mL of basal growth medium (see below) and minced into 1- to 2-min pieces. Tissue fragments were then seeded into appropriate culture containers.

Various enzymes were employed for the disaggregation of cells from oyster tissues. Effectiveness of pronase (0.25%), trypsin (0.25%), collagenase (0.25% or 250 U/mL), and hyaluronidase (0.01%) was evaluated. Enzymes were dissolved in Earle's saline with additional salts (Li et al. 1966) and antibiotics (see saline rinse above for composition). Ten millilitres of this enzyme solution were used for each gram of tissue.

The tissue was gently agitated in the enzyme solution for a period of 1.5–2 h at 28–30°C. After dilution with an equal volume of basal growth medium, aliquots were distributed into sterile screw-capped centrifuge tubes. The suspensions were centrifugated at 120 × *g* for 15 min and the pellet resuspended in the appropriate growth medium. Cell density was measured with a hemocytometer, and adjustment was made to 5×10^4 cells/mL before aliquots were dispensed into culture vessels.

Larvae were disrupted by shaking rigorously for 30 min at 20°C in a constant temperature water bath equipped with a reciprocating mixer. The resulting suspension was then centrifuged for 25 min at 120 × *g*, and the pellet was resuspended in growth medium. Aliquots were distributed to growth vessels with no adjustment of cell numbers.

Culture maintenance — All cultures were incubated in sealed containers except when a CO_2-enriched atmosphere was used. A pH of 7.0–7.3 was maintained for all cultures, except primary embryo cultures, with periodic readjustment using 10% $NaHCO_3$. Carbon dioxide enriched atmospheres were produced either in a continuous flow CO_2 incubator, or in a sealed vacuum jar into which CO_2 was injected through a rubber hose with a needle and syringe.

Embryo cultures were maintained at a more alkaline pH of 7.8–8.0, which is similar to the pH found in seawater. Sealed containers were used, and the pH periodically adjusted with sodium bicarbonate solution.

Temperatures of 12, 20, and 28°C were evaluated. The 12 and 20°C values were attained using thermostatically controlled, refrigerated incubators. The 28°C condition was maintained by immersing a vacuum jar incubator into a constant temperature water bath adjusted to that temperature. All culture media evaluations were done at 20°C.

Plastic flasks (Falcon 30 mL) or 24-cell plastic microtiter plates (Falcon) were routinely utilized for culturing both explanted and enzyme-treated cells. Leighton tubes containing glass or plastic coverslips were also used on occasion.

Media change was routinely done once every 3 wk. The use of conditioned media was tried but not regularly utilized.

Media formulation — The basal medium employed was that of Li et al. (1966). A 2X solution of this was produced by dissolving 1 L of powdered Medium 199 with Earle's salts and L-glutamine into 500 mL of marine saline (Li et al. 1966). Penicillin (100 U/mL final concentration), streptomycin (100 μg/mL), and amphoericin B (2.5 μg/mL) were used routinely.

Additives were used in combination with the basal medium to form definitive growth media. The study was initiated with a basic series of six media (Table 1). Fetal calf serum was substituted for an equal volume of basal medium diluent (water) thus forming medium 1, which was used as a stock solution. Other modifications were made sequentially as noted by using growth factor solutions in addition to, and not as a substitution for, basal medium diluent. Medium 3 was used as a secondary base medium and media 4, 5, and 6 are examples of typical modifications. Embryo cultures were maintained in the growth medium described in Table 2.

Oyster extracts — Extracts of oyster tissues were produced by adding standard portions of tissue to marine Earle's saline and grinding using a tube and piston type tissue grinder. The resulting solution was then centrifuged at 12 000 × *g* for 30 min and the supernatant decanted and filter sterilized through a 0.22-μm (H.A.) Millipore filter. All extracts were heat-inactivated at 60°C for ½ h.

Hemolymph was removed from the pericardial cavity with a sterile plastic disposable syringe at the time of heart removal. A total of 3–5 mL of hemolymph was routinely obtained from each oyster. Following heat inactivation at 60°C for 30 min, the hemolymph was centrifuged at 12 000 × *g* for 15 min, and filter sterilized through a 0.22-μm Millipore filter. Hemolymph was stored at —20°C and was routinely assayed for bacterial contamination before use. Only hemolymph that exhibited the pale "phosphorescent" blue coloration was used; cloudy or flocculent hemolymph was discarded.

TABLE 1. Media compositions.

Medium 1:	Basal medium	85 mL
	Fetal calf serum[a]	15 mL
		100 mL
Medium 2:	Medium 1	100 mL
	Lactalbumen hydrolysate[a] (10% sol'n)	5 mL
		105 mL
Medium 3:	Medium 1	100 mL
	Lactalbumen hydrolysate (10% sol'n)	5 mL
	Oyster hemolymph	10 mL
		115 mL
Medium 4:	Medium 3	100 mL
	Beef embryo extract[a]	5 mL
		105 mL
Medium 5:	Medium 3	100 mL
	Whole oyster extract	10 mL
		110 mL
Medium 6:	Medium 3	100 mL
	Oyster heart extract	10 mL
		110 mL

[a] GIBCO, Grand Island, New York, N.Y.

Salines — Several other salines were utilized in addition to the routinely used marine Earle's saline with additional salts as described by Li et al. (1966). These were made up in 2X concentrations to which were added MEM amino acid and MEM vitamin concentrates (GIBCO) to make up the basal medium. Salines used were those of Cameron (1950), Tripp (1963), and artificial seawater (Instant Ocean). These were evaluated by substitution into media 3 and 6 as well as basal medium. A series of four explants were used in each medium, and time until culture demise was noted.

In addition, Earle–Li saline was modified by changing the ratio of sodium to potassium. Basal medium was prepared as described previously. Saline was produced by preparing an Earle's–Li saline base without NaCl and KCl, and by adding varying amounts of standardized NaCl or KCl solutions to alter the Na:K ratio. Total salt concentrations were identical for every combination. No additives were used in testing these salines, and all tests were compared to controls of unaltered basal medium. Ratios (Na:K) of

TABLE 2. Larvae cell culture.

Oyster embryo extract	5 mL
Fetal calf serum	10 mL
Algal hydrolysate[a]	5 mL
Oyster hemolymph	2 mL
Antibiotics (pen.-strept.-ampho. B)	1 mL
Seawater	100 mL

[a] Suspensions of algae (primarily genus *Isochrysis*) were disrupted by sonic oscillation and heated at 100°C for 15 min in 0.1 NHCl, followed by neutralization with 1N NaOH and filtration through a 0.22-μm Millipore filter.

35:1, 40:1, 45:1, 50:1, 55:1, 60:1, 75:1, and 100:1 were tested by observing maximum culture time lengths as with the above substitute salines.

Evaluations of supplements—All test additives were subjected to a standard assay procedure utilizing heart explants to determine the usefulness of the additives in maintaining culture quality. Since different hearts varied considerably in the quality of the cultures they produced, some standardization was attained by using quarter sections of hearts as explants Each quarter was grown in a separate well of a 24-well microtiter plate. After an initial 24-h period of growth in medium 3, the medium was changed to the test medium. Only cultures of excellent (4+) quality after the initial 24-h growth period were used for assay.

Cultures were observed every 2–3 d, and their quality was recorded after 1, 3, 7, 14, 21, and 42 d of culture in the test medium. Ratings were made on a 1+ (poorest) to 4+ (best) scale. Cultures were monitored until no signs of extended or metabolizing cells could be observed for 4 consecutive days. Each medium was tested on tissue from at least two different hearts, and a minimum total of six tests were performed. Medium 3 and medium 6 were always run as reference controls for each heart, thus leaving a maximum of two explants per heart available for assay. Total time from initiation to deterioration was noted for each test.

Results — Heart tissue culture — Heart tissue yielded the most easily obtained and most consistently noncontaminated cultures. For these reasons, the majority of the work in this study was devoted to this tissue. Occasionally, mantle and other tissues were cultured for comparative purposes.

All heart explants underwent a similar initial series of events when cultured in various growth media at 20°C. Within the 1st d of explant three distinct zones of cells were established. Closest to the explant and extending outward from it up to 4 mm, depending on explant size, was an area of densely packed cells, zone I (Fig. 1). These were cells that had recently migrated out of the explant. Individual cells appeared to reside here only transiently before extending and moving farther away from the explant. The rounded nature of the cells might represent a response to contact and cell density since smaller explants with fewer shedded cells were often surrounded by zones of fully extended cells.

Immediately outside of zone I, a narrow band (zone II) of single and clumped cells was observed (Fig. 2). These cells exhibited an extended form more typical of oyster amoebocytes. Cell clumps formed from the aggregation of many motile amoebocytes, and were often not firmly attached to the substrate.

The third discernible zone was at the periphery of the cultures and consisted of a mixture of extended and rounded single cells in various metabolic states (Fig. 3). Occasionally small clumps developed here early in the culture life similar to those in zone II. Near the edge of the culture vessel there was a tendency for cells to pile up and take on a rounded form similar to zone I cells. These cells were less active metabolically as exhibited by (1) lack of motility of filiform appendages when present, (2) lack of highly active intracellular Brownian-like movement typical of younger cells, and (3) failure to take up vital dyes. A higher proportion of nonextended cells occurred with increasing distance from the explant. No evidence of cell division was obtained even following exposure to mitomycin C and phytohemagglutinin; however, explants could be broken up and used to initiate new cultures as described below.

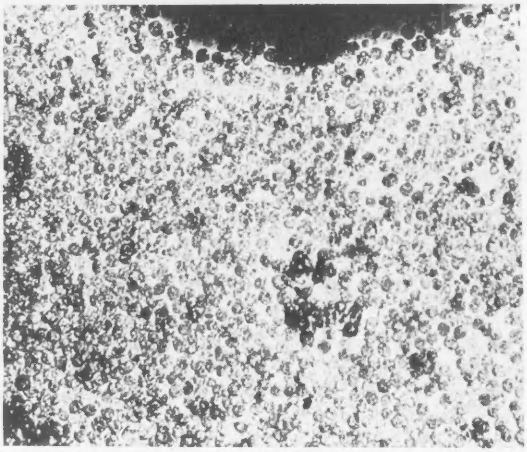

FIG. 1. Oyster heart explant culture exhibiting densely packed, rounded cells immediately adjacent to the explant (zone 1). ×200

Confluent cell cultures were usually obtained within 7–14 d, under optimum conditions. Virtually all viable cells consistently appeared to be granular or agranular amoebocytes, with granular cells predominating. Electron microscopic examination confirmed the predominating cells to be granular amoebocytes similar to those described by Cheng (1975).

Cell cultures were also initiated with enzymatically dissociated heart tissue. Best results, as judged by the relative numbers of viable cells, were obtained with a solution of collagenase and hyaluronidase. Trypsin and pronase were too harsh on oyster cells even during relatively short periods of treatment, with few viable cells surviving. In general, the cultures obtained were similar to those at the periphery of explant cultures with amoebocytes predominating. Enzyme dissociated cultures, however, could not be maintained as long as explant cultures.

Oyster larvae tissue culture — In an attempt to obtain actively dividing cells, in vitro cultures from disaggregated larvae were initiated (Fig. 4). The predominant feature of these cultures was the presence of large "balls" of cells attached to the vessel surface. No single cells or cell monolayers were observed. These "balls"

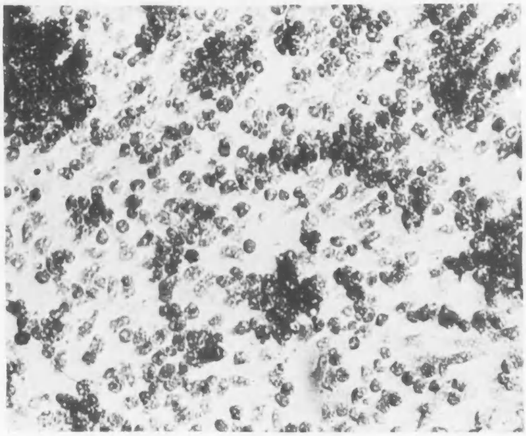

FIG. 2. Oyster heart explant culture exhibiting cells away from the explant (zone II). ×200

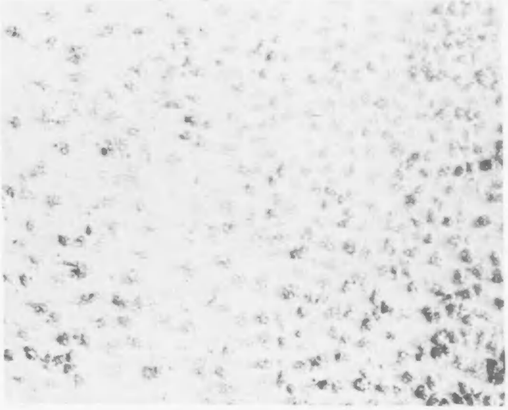

FIG. 3. Oyster heart explant culture exhibiting mixture of extended and rounded cells at periphery of culture (zone III). ×150

of embryonic cells increased in size and cell numbers with time with the occurrence of cell division. Unfortunately, these cultures succumbed to microbial contamination in the 2nd wk.

Comparison of different growth media — Sections of oyster heart from the same animal were explanted into appropriate vessels and incubated in the various media. The cultures were observed daily and their relative viability noted. In addition, the average and maximum lengths of time viable cells were maintained were determined for at least six cultures incubated in each medium. As indicated in Table 3, most media did not differ significantly in the maintenance of oyster heart cells for relatively short periods of time (1–4 d), with the exception of medium 5 which contained whole oyster extract and was obviously toxic to the cells. The various media did differ significantly, however, with regard to the length of time the cultures could be maintained. Media 4 and 6 were obviously superior; medium 6 maintained viable cells for up to 6 mo with an average duration of 85 d. Figure 5 depicts viable amoebocytes surrounding a small explant 6 mo after initiation.

Previous attempts to subculture cells have been unsuccessful. However, explants maintained in medium 6 could be mechanically disrupted and transferred to other vessels with the subsequent initiation of new cultures. Such cultures, however, could not be subcultured indefinitely.

Optimum temperature and pH — Evaluation of pH and temperature requirements using similar procedures and employing medium 6 indicated that pH 7.0–7.3 at 20°C were optimal; incubation above 27°C resulted in rapid cell death.

TABLE 3. Evaluation of various media for maintenance of amoebocyte cultures.

							Survival time (d)	
	Day 1	Day 3	Day 7	Day 14	Day 21	Day 42	Avg	Maximum
Saline	4+[a]	2+	0	0	0	0	4[b]	6
Basal Medium	4+	2+	0	0	0	0	4	7
Medium 1	4+	3+	2+	±	0	0	10	17
Medium 2	4+	3+	2+	1+	0	0	14	19
Medium 3	4+	3+	2+	2+	±	0	22	29
Medium 4	4+	3+	2+	2+	2+	2+	53	104
Medium 5	2+	0	0	0	0	0	2	2
Medium 6	4+	3+	3+	2+	2+	2+	85	187
Medium 6 (Enzyme-treated cultures)	4+	3+	3+	2+	2+	0	26	32

[a] Cultures were observed daily and their relative viability scored on a scale from 0 to 4+, the latter comparing to the best newly initiated cultures in terms of relative cell numbers and activity.

[b] Results represent averages of six experiments.

FIG. 4. Oyster larvae tissue culture exhibiting masses of large "balls" of actively dividing cells. ×63

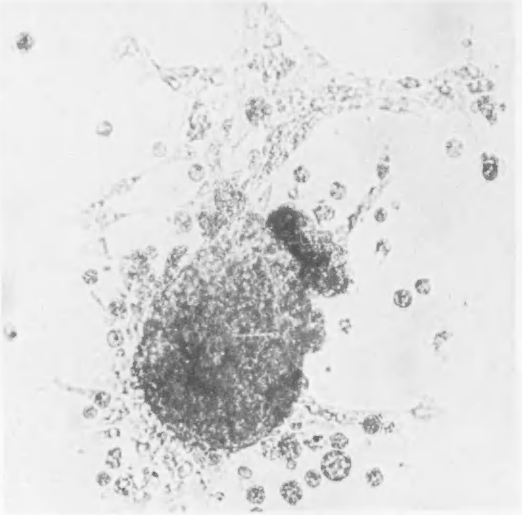

FIG. 5. Viable amoebocytes in heart explant culture 6 mo after initiation. ×275

Saline composition and sodium/potassium ratio — Evaluation of four different saline formulations including artificial seawater as described in the *Materials and methods* indicated no significant differences in average or maximum maintenance of amoebocyte cultures. In addition, Earle–Li saline was modified by changing the ratio of sodium to potassium. This was attempted in response to the possibility that such ratios may play a role in invertebrate cell culture as reported by Jones (1966). Varying the Na:K ratio of the basal medium over a range of 35:1 to 100:1 had no apparent effect on culture quality or maintenance.

Discussion — The results of this investigation confirm those of other studies and add to our capabilities to maintain oyster cells in vitro. Cultures produced from explants of heart tissue (1) consisted almost entirely of actively motile, granular amoebocytes, (2) generally lasted from 2–4 mo under optimal conditions, (3) yielded no mitotic cells, and (4) could be subcultured by mechanical disruption of the explants.

Amoebocyte cultures underwent a characteristic sequence of events, i.e. an early peak in culture quality followed by a variable maintenance period depending on the medium used. A zone of tightly packed, round cells immediately surrounding the explant probably resulted from the continued "shedding" of large numbers of cells from the explant. The second zone of extended cells may be viewed in terms of the reaction of explanted amoebocytes to the new and foreign environment outside the heart tissue. Typical of this zone were clumps of amoebocytes. Clumping has been observed by several researchers, especially in conjunction with healing wounds (Ruddell 1971). In that capacity, amoebocytes perform a dual function of "clot-formation" and "walling-off" of foreign objects such as parasites. The reasons for such clumping in vitro are unclear. Clumping also occurred in saline without additives. Possibly, aggregates of these highly phagocytic cells form around organic matter or dead cells that have collected around the explant. This would explain the increase in clumping which occurred with increasing age of cultures.

In the outermost zone, cells carried on a "foraging" type of existence by moving about and phagocytically engulfing debris. Here a mixture of cells in various stages of metabolism coexisted.

It is unclear whether cell division was occurring in explant cultures. No cell division was observed in cells migrating away from explanted tissue, even after exposure to several mitogens. However, cultures were maintained in the optimal medium for periods up to 6 mo with continuous shedding of cells from the explant. Possibly, cell division was occurring within the explant itself. In media supplemented with oyster hemolymph and heart extract, explants could be broken up and transferred to other vessels with the subsequent initiation of new cultures; however, such cultures could not be subcultured indefinitely. Also, even in actively growing tissues such as those surrounding wounds, the rate of mitosis in oyster tissues is very low with <5 mitotic figures/1000 (Hillman 1963).

Of the adult tissues tested, oyster hearts provided the most reliable source of uncontaminated cells for use in culture. Other researchers (Perkins and Menzel 1964) have made use of mantle tissue explants, although in this study considerable problems were encountered with contamination in this tissue.

Enzymatic digestion provided a viable alternative for producing primary cell cultures from oyster tissues. Collagenase and hyaluronidase in combination were the most efficacious. Trypsin and pronase treatment were unsuitable with few viable cells surviving. However, long-term survival in the optimal medium was drastically curtailed by this procedure. This fact may limit the usefulness of this technique for routine culture in the future.

Our results extend those of other studies with regard to optimal composition of growth medium for the maintenance of oyster explant cultures. It was known that basic requirements for prolonged maintenance of amoebocytes included a seawater-like saline supplemented with animal sera, protein digests, and/or vertebrate culture media of various sorts. We demonstrated that further increases in maintenance time can be provided by the addition of oyster hemolymph and oyster heart extract.

We demonstrated that oyster amoebocytes in vitro are highly tolerant of a wide variety of environments in terms of survival and motility. Thus amoebocytes tolerated relatively wide variations in saline, medium composition, pH, and temperature. Possibly these conditions could be refined to improve the duration and quality of cultures.

Larval tissues were the most promising of those tested for possible establishment of continuous cell lines. The numbers of cells in such cultures rapidly increased in a relatively short time (1–7 d). However, the establishment of cultures free of contamination presented a serious problem. This might be remedied by the application of special measures in the breeding of adults, perhaps even to the point of obtaining eggs and sperm surgically and controlling their environment while fertilization and initial growth occurs. Larvae have successfully completed development under conditions free from bacterial contamination with the use of antibiotics (Millar and Scott 1967).

Efforts should be maintained to establish continuous cell lines from oyster and other molluscs. Such cell cultures would greatly enhance studies of molluscan disease and physiology. Meanwhile, primary cultures of oyster hemacytes should be evaluated for ability to support the replication of oyster, and other viruses. This work has demonstrated that such primary cultures with the capability of limited subculture can be routinely initiated free of contamination and maintained for relatively long periods.

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Pygmy Whitefish, *Prosopium coulteri*, in Three Lakes of the Copper River System in Alaska

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BIRD, F. H., AND K. ROBERSON. 1979. Pygmy whitefish, *Prosopium coulteri*, in three lakes of the Copper River System in Alaska. J. Fish. Res. Board Can. 36: 468–470.

Pygmy whitefish (*Prosopium coulteri*) were recorded for the first time from the Copper River drainage in Alaska (from Tazlina, Klutina, and Tonsina lakes). Morphology of the specimens indicate affinity to the Lake Superior and Waterton Lake populations, falling outside the ranges previously established for "low-rakered" and "high-rakered" forms found in Alaska. Based on geographical proximity, however, probable origin for these fish is from an upper Yukon River unglaciated refugium.

Key words: pygmy whitefish, Copper River, Alaska, morphology, Yukon River, unglaciated refugium

BIRD, F. H., AND K. ROBERSON. 1979. Pygmy whitefish, *Prosopium coulteri*, in three lakes of the Copper River System in Alaska. J. Fish. Res. Board Can. 36: 468–470.

Nous signalons pour la première fois la présence de ménominis pygmées (*Prosopium coulteri*) dans le bassin hydrographique de la rivière Copper, en Alaska (dans les lacs Tazlina, Klutina et Tonsina). Par leurs caractères morphologiques, les sujets sont apparentés aux populations du lac Supérieur et du lac Waterton, et se situent en dehors de limites établies antérieurement pour les formes à «branchicténies peu nombreuses» et à «branchicténies nombreuses» trouvées en Alaska. A cause de la proximité géographique, cependant, l'origine probable de ces poissons est un refuge non touché par les glaciers du haut-fleuve Yukon.

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THE pygmy whitefish, *Prosopium coulteri*, is a small, large-scaled fish displaying a highly disjunct distribution. In Canada it is found in the Columbia, Fraser, Skeena, Peace, Liard, and Yukon River systems and in Elliot and Waterton lakes. In the United States they occur in the Columbia River system, Lake Superior, and in the Bristol Bay and Chignik systems in southwestern Alaska. It was originally thought to make up one homogenious species (Eshmeyer and Bailey 1955), but McCart (1970) showed that two or more forms exist sympatrically in several Bristol Bay lakes. Heard and Hartman (1965) studied the biology of pygmy whitefish in the Naknek River system of southwest Alaska, but made no effort to differentiate between possible sympatric forms. Since the work of McCart no additional occurrences of pygmy whitefish in Alaska have appeared in the literature.

This note describes the recent collection of pygmy whitefish from three Alaska lakes, extending the known range into the Copper River Basin (Fig. 1).

Collection area description — Collections were made from Tazlina, Klutina, and Tonsina lakes which are large glacial lakes located on the north side of the Chugach Mountains in southcentral Alaska. Each lake is part of a separate basin that drains into the Copper River. The Copper River Basin is contiguous to the Yukon River via the Nabesna–Tanana rivers on the north and east sides, making it the closest known occurrence of pygmy whitefish to the Copper River Basin.

The three lakes lie between 61°30′N–62°00′N and 145°30′W–146°30′W, ranging in elevation from 524 to 575 m, in size from 1392 to 15 378 ha and in maximum depth from 95 to 115 m. All carry glacial silt with turbidity levels from 26.0 to 92.5 Nephelometric Turbidity Units (Roberson et al. 1978).

Specimen collection — Fish species taken by beach seine or monofilament gill net from shore were, in all three lakes: *Prosopium coulteri*, *P. cylindraceum*, *Thymallus signifer*, *Oncorhynchus nerka*, and *Cottus spp.*; in Tazlina and Klutina: *Catostomus catostomus*, *Salvelinus malma*; in Tazlina only: *Salmo gairdneri*, *O. tshawytscha*; in Klutina and Tonsina: *O. kisutch*, *Coregonus clupeaformis*, *Lota lota*, and *Salvelinus namaycush*. All specimens were collected between July 13 and September 21, 1977.

Biology — Pygmy whitefish in these three lakes attain sexual maturity during their 2nd yr with spawning occurring sometime after September. Fecundity for two Tazlina Lake females, 120 mm (FL), 19.7 g and 104 mm, 12.6 g, was 290 and 200 eggs, respectively. Two Klutina Lake females, 90 mm, 8.4 g and 81 mm, 5.7 g, contained 138 and 104 eggs, respectively. Age–length data shows that growth was slower than in other lakes where pygmy whitefish are found (Scott and Crossman 1973). Age (yr)–length (FL, mm)

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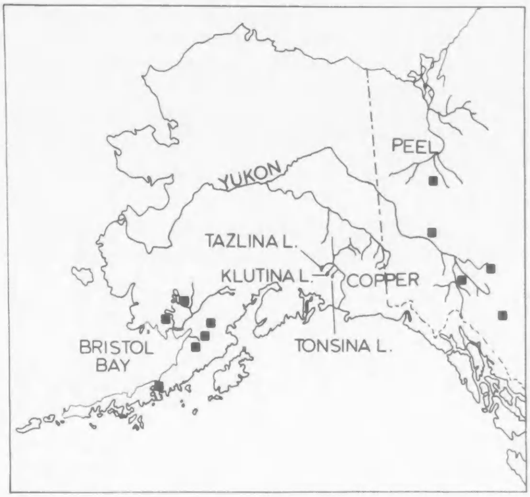

FIG. 1. Geographic distribution of pygmy whitefish in northwest Canada and Alaska (■) plus location of recent collections from Tazlina, Klutina, and Tonsina lakes, Alaska.

for the three lakes were Tazlina 1-58, 2-75, 3-92, 4-100, 5-120; Klutina 0-37, 1-61, 2-70, 3-84, 4-81; Tonsina 1-71, 2-83. All fish were taken from water <1 m deep; no attempt was made to obtain specimens from deeper waters.

Morphology — Pygmy whitefish from the three lakes are similar to specimens examined by McCart (1970), Lindsey and Franzin (1972), Eschmeyer and Bailey (1955), and Heard and Hartman (1965). On the basis of counts (Table 1), specimens from these lakes are similar, though Klutina Lake specimens differ in gill raker counts. All specimens possessed a rudimentary pelvic axillary process.

Discussion — On the basis of the ratio of gill rakers to caudal peduncle scale rows, the specimens from the three lakes do not fall into either the "low-rakered" form from the Peace, Skeena, Fraser, Columbia river and some localities in the Bristol Bay region, or into the "high-rakered" form from the Liard and Yukon River drainages and some localities in the Bristol Bay region (Fig. 2). Based on this grouping (McCart 1970; Lindsey and Frazin 1972) the pygmy whitfish from Tazlina and Tonsina lakes more closely resemble Lake Superior specimens while those from Klutina Lake more closely resemble the Waterton Lake population. This is an interesting grouping considering that Klutina lies between Tazlina Lake (34 km to north) and Tonsina Lake (37 km to the south).

That the populations of pygmy whitefish existed in these three lakes during the last glaciation is unlikely since the entire Copper River Basin was one continuous ice sheet during this period (Schuchert and Dunbar 1941). Considering the geographical barriers separating the Bristol Bay populations from the Copper River

TABLE 1. Morphology of pygmy whitefish taken from three Alaska lakes in 1977.

	Tazlina Lake	Klutina Lake	Tonsina Lake
Pectoral ray (*n*)	14	20	4
Mean	13.9	13.9	14.5
Range	13–14	13–15	13–15
Pelvic ray (*n*)	14	20	4
Mean	9.2	9.1	9.3
Range	9–10	9–10	9–10
Dorsal ray (*n*)	14	20	4
Mean	11.0	11.4	11.3
Range	10–12	11–12	10–12
Anal ray (*n*)	14	20	4
Mean	11.4	11.9	11.5
Range	10–12	10–12	11–12
Lateral line pored scales (*n*)	14	21	4
Mean	56.6	55.5	57.0
Range	53–62	53–58	56–58
Gill rakers (*n*)	4	4	4
Mean	15.3	17.5	15.3
Range	14–16	17–18	14–16
Caudal peduncle scales (*n*)	4	4	4
Mean	16.3	16	16
Range	16–17	15–18	16

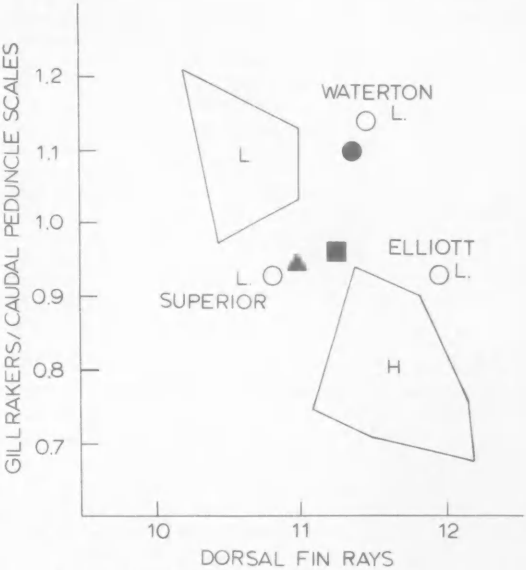

FIG. 2. Relationship between population means of dorsal fin ray counts and ratio of number of gill rakers to that of caudal peduncle scale rows. Enclosures include high-rakered forms (H) and low-rakered forms (L). ▲, Tazlina Lake; ○, Klutina Lake; ■, Tonsina Lake. Adapted from Lindsey and Franzin 1972.

populations, introduction from a Bristol Bay refugium is improbable. This leaves a Yukon River refugium as the most probable source of Copper River pygmy whitefish.

Evidence for a Yukon River origin is primarily geological, since morphologies of the two groups are dissimilar, though not extremely so. Assuming a broader distribution of pygmy whitefish in the Yukon River during and immediately after glaciation, crossover into the Copper River by stream capture could easily account for the introduction into the Copper River Basin of pygmy whitefish as well as the several other nonanadromous species now found there. There is now one location within the Copper Basin where stream crossover of a tributary of the Copper River into a tributary of the Yukon River has occurred within the last 50 yr.

The variation in morphological characters between the Copper Basin and Yukon River population of pygmy whitefish can probably be accounted for by the natural variation occurring within postglacially isolated stocks. This would also account for the slight variation in morphology between Copper Basin lakes.

Present geographical distribution of the fish within the basin can be explained in terms of past glacial activity. At the time of glacial recession, and probable simultaneous transfer of pygmy whitefish into the basin, most streams and lakes were glacial, as many are now. This provided the pygmy whitefish with a means of dispersal through a habitat similar to that in which it now occurs in the Copper Basin. Why distribution within the basin is restricted to three deep glacial lakes when many large, clear deep lakes are present is a matter for speculation. Possibly, predator pressure or other habitat related pressures eliminated these low-fecundity fishes in the clearer lakes. Also, because of sampling difficulty, it is possible the presence of these fish in other waters has so far been missed.

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Indices of Food Type Preference by a Predator

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PALOHEIMO, J. E. 1979. Indices of food preference by a predator. J. Fish. Res. Board Can. 36: 470–473.

The forage ratio and Ivlev's electivity index as measures of preference by predators of different prey or food types were shown by Jacobs to depend on their abundance. Modifications proposed by Jacobs are shown here to be similarly affected by the abundance. However, an index of the preference that is indeed independent of the prey abundance can be based on standardized forage ratios, standardized so that the forage ratios for the different prey species sum to one.

Key words: index of preference, prey selection, food selection, predator–prey relationship

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Jacobs a démontré que le rapport de recherche de la nourriture et l'indice d'électivité d'Ivlev utilisés comme mesures de préférence, de la part des prédateurs, de différents types de proies ou d'aliments dépendent de l'abondance de ces derniers. Nous démontrons ici que les modifications proposées par Jacobs sont, elles aussi, affectées par l'abondance. Cependant, un indice de préférence réellement indépendant de l'abondance des proies peut être fondé sur des rapports de fourrage normalisés de façon que la somme de ces rapports pour les différentes espèces proies égale un.

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AN ecologist studying the predation and food preferences of a predator usually has no way of measuring the preference directly but has to rely on identification of different prey species consumed. The total consumption by the predator is dependent on the abundance of the prey, on the capacity of the predator to consume prey, and on many other factors besides its preference for different prey species. Before an index of preference can be constructed, the role of the abundance and the capacity of the predator to consume and their effect on the total numbers of prey taken must be clearly understood.

Two of the most commonly used indices of preference of food selection are Ivlev's index of electivity (E) (Ivlev 1961) and forage ratio (FR) (Shorygin, cf. reference in Ivlev 1961). These have been used by a number of ecologists to quantify the process of food or prey selection by a predator (e.g. Confer and Blades 1975; Hutchinson 1971; and Neill 1975). Jacobs (1974) showed that the two indices are not appropriate measures of prey selection since they both depend on the abundance of prey and not just on the predators preference. Jacobs proposed two new indices that he claimed were not distorted by changing proportions of resource types in the environment.

Ivlev's and Shorygin's indices of preference were based perhaps on an intuitive notion. Jacobs derived his formulae by examining the mortality rate generated by the predator on its prey. I believe that this is not a reasonable way to look at the situation; the mortality of any prey species may fluctuate widely and independently of the grazing by the predator whose food selection is being examined. Moreover, in many studies the samples are taken over a relatively short time interval when the abundance of the different food items is relatively constant. Indeed, in calculating the ratio of particular food in the diet to the food in the environment (forage ratio), this assumption is explicitly made.

My objective was, therefore, to show, using a simple, but perhaps not too unreasonable model, that the forage ratio and Ivlev's selectivity do indeed depend on the prey abundance. The modifications proposed by Jacobs do not correct the situations except when the predator has a limited diet of no more than two species of prey. However, a simple alternative based on standardized forage ratios may be used as an index of relative preference.

Rationale — Although I will present the reasoning in a mathematical framework, the conclusions are simple and obvious. We can only compare the predator's relative preferences for different prey species. These relative preferences are obtained from the ratio of numbers of prey caught to the abundance of that prey type. These ratios are proportional to the preference by the predator for the given prey type and they may be adjusted to add to one to arrive at the relative "preferences" for each type of prey. Moreover, the "preferences" are, as commonly acknowledged, composite indices expressing not only the preference but ease of capture, and the detectability of the prey to the predator.

The derivation that I present assumes a random distribution of each prey species selected by the predator. Where clumping or clustering of prey occurs, the index may be distorted showing either more or less preference to the particular prey species, depending on the relative detectability of clusters of prey as opposed to single specimens. Moreover, the prey are assumed to be "rare" enough relative to their detectability by the predator so that the predator has to search for the prey. If the predator of some abundant prey species can in fact proceed from one prey item to its nearest neighbor without having to search for its next victim of that prey type, quite different considerations apply. In this case, when no searching is involved, the numbers of prey taken must be divided by the square root of their abundance (Paloheimo 1971) to arrive at a meaningful forage ratio. In practice this may well be important although somewhat difficult to quantify.

Indices of preference — We suppose that there are n prey species selected for by a predator. Following Ivlev and others we let r_i = proportion of prey $_i$ in the diet and p_i = proportion of prey $_i$ in the environment. Note that in calculating p_i we include only those resources that are being utilized by the predator in question. The forage ratio and electivity are now defined as

$$FR_i = \frac{r_i}{p_i},$$

$$E_i = \frac{r_i - p_i}{r_i + p_i}.$$

Jacobs suggested that the above should be replaced by indices that are independent of the density of the prey. His indices are

$$Q_i = \frac{r_i(1-p_i)}{p_i(1-r_i)},$$

$$D_i = \frac{r_i - p_i}{r_i + p_i - 2r_ip_i}.$$

It can be readily seen that E_i can be calculated from FR_i and vice versa. Similarly D_i can be calculated from O_i and vice versa. There is no point having two indices when one will do.

Model based on search theory — We now assume that each prey species is randomly distributed in the general area searched by the predator. Let

λ_i = density of prey, $i, i = 1, \ldots, n$
R_i = average area or volume searched by the predator per unit time in relation to the i^{th} prey
P_i = probability of capture of the i^{th} prey once sighted
τ = delay and handling time per capture of the i^{th} prey.

Note that the R_i, the average area or volume searched, depends on the vector sum of the speeds of the predator and prey (Skellam 1958), and on the radius of detection of prey by the predator. Hence R_i may be different for each species of prey. The term P_i combines what might be called "preference" and the ease of capture. Thus, if half of the prey attacked will escape and if half of the prey sighted are ignored, $P_i = \frac{1}{2}\cdot\frac{1}{2}$. Note also that we have chosen to ignore the delay time associated with the persuit and escape of prey. It can be included but it will only complicate the equations unnecessarily.

When there is only one prey species involved ($n = 1$) it can be seen (e.g. Paloheimo 1971) that

$$\text{searching time per successful capture} = 1/\lambda_1R_1P_1$$

and hence the number of prey caught per unit time

$$= 1/(1/\lambda_1R_1P_1 + \tau_1)$$
$$= \lambda_1R_1P_1/(1 + \lambda_1R_1P_1\tau_1)$$

This is the familiar Monod equation, Hollings disk equation, number of renewals in a given period, etc., showing the functional response of the predator to prey density. In the case of n prey we get

$$\text{(1)}\qquad \begin{array}{c}\text{no. of prey } i \text{ caught}\\ \text{in a unit time}\end{array} = \lambda_iP_iR_i/\left(1 + \sum_{j=1}^{n} \tau_j\lambda_jR_jP_j\right)$$

This may be derived as follows:
Total average searching time per prey is $1/\Sigma\lambda_jR_jP_j$ and delay time $\Sigma\tau_j\lambda_jR_jP_j/\Sigma\lambda_jR_jP_j$, the sum of the two is total time per prey; the inverse of the sum is the number of prey caught per unit time, this is now multiplied by the conditional probability $\lambda_iR_iP_i/\Sigma\lambda_jR_jP_j$ that the prey caught is of type i to give the equation (1).

The main point is that the number of prey of type i caught is proportional to their density

$$\text{(2)}\qquad \text{number of prey } i \text{ caught/unit time} \sim \lambda_iR_iP_i$$

where R_i depends on the detectability of prey i and P_i is the probability of capture multiplied by the preference index. Any index that we may obtain based on the observed numbers caught is always bound to be a function of preference, detectability, and ease of capture.

Because electivity is an algebraic function of forage ratio, and Jacobs' D a simple function of Q, we shall look at the forage ratio and Jacob's Q only. Simple calculations using equation (2) show that the proportion of prey i in the diet and in the environment are given

$$r_i = \lambda_iR_iP_i\Big/\sum_1^n \lambda_jR_jP_j$$

$$p_i = \lambda_i\Big/\sum_1^n \lambda_j$$

Hence, the forage ratio and the index Q of prey i are

$$\text{(3)}\qquad FR_i = R_iP_i\sum_1^n \lambda_j\Big/\sum_1^n \lambda_jR_jP_j$$

$$Q_i = R_iP_i\sum_{j\neq i} \lambda_j\Big/\sum_{j\neq i} \lambda_jR_jP_j$$

The summations in the equation for Q_i are from 1 to n omitting the i^{th} term.

We note the close similarity between the two indices. On the basis of the above equations it is difficult to say which one to prefer, both depend on the density of the prey organisms except when $n = 2$. When the number of prey in the diet is no more than two, we get

$$FR_1 = R_1P_1(\lambda_1 + \lambda_2)/(\lambda_1R_1P_1 + \lambda_2R_2P_2)$$
$$Q_1 = R_1P_1/R_2P_2$$

and similarly for FR_2, Q_2.

The apparent, observed preferences or selectivities may be taken to be equal to R_iP_i. How well the forage ratio and Q reflect the apparent selectivities can perhaps be best illustrated by example calculations of forage ratio and Jacobs' Q for three prey types with varying densities shown below.

	Estimated "selection"			
Prey	RP	λ	FR	Q
		Case 1		
1	0.1	1	0.3	0.22
2	0.3	1	0.9	0.85
3	0.6	1	1.8	3.00
		Case 2		
1	0.1	3	0.4	0.25
2	0.3	2	1.2	1.33
3	0.6	1	2.4	3.11
		Case 3		
1	0.1	1	0.24	0.21
2	0.3	2	0.72	0.65
3	0.6	3	1.44	2.57

From the above table or from equation (3) a number of things are obvious. First of all, when the densities are fixed, both indices reflect the order of "selectivity" correctly. Secondly, the forage ratio is exactly proportional to the apparent selectivity while the Q is not. However, the proportionality factor varies with the densities for prey species. If the forage ratios are standardized so that they add to one, these standardized forage ratios are always proportional to the apparent selectivities, denoted here by R_iP_i for prey i. These standardized forage ratios are independent of prey densities. No other measures of selectivity or preference other than relative measures are possible unless such things as the radius of detection of prey i by the predator, the probability of capturing the prey sighted, the distribution of prey, etc., are known.

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BOOK REVIEWS/COMPTES RENDUS

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Coastal Resources Management. *Robert B. Ditton, John L. Seymor, Gerald C. Swanson. Lexington Books, D.C. Heath and Co., Lexington, Mass. 1977. xvi + 196 p. $17.50 U.S.*

The coastal zone is regarded as the "interface between the land, the sea, and the atmosphere." It encompasses the ocean, including submerged land, and shorelands that drain directly into coastal waters, including coastal floodplains, uplands of the floodplains, wetlands, and intertidal areas. Coastal resource management is concerned with efficiency and equity in the use of coastal zone resources and with the roles and responsibilities of the public sector and the private sector in making resource allocation decisions.

The growing concentration of human populations on the coastline of the United States accompanied by urban and industrial growth and development is regarded as a "disruptive force" which adversely affects the "endemic" coastal resources through the modification of the natural habitat. In this regard, man appears to be portrayed, not as an integral part of the natural environment, but as a coastal parasite who through growing numbers is creating adverse changes to ecological systems with resultant losses of coastal resources.

Regional growth and development, the process generally regarded as responsible for environmental degradation, is at the same time the force that is largely responsible for enhancing society's leisure time and disposable income to enjoy the environment. Coastal resource management explores the tools available from the disciplines of law, economics, political science, and administration to allocate resources and mitigate the disruption of man's activities on the environment.

The authors acknowledge a division of labor between the public and the private sector in the provision of goods and services. At the same time, concern is registered for market failures which lead to suboptimal resource allocation decisions. A major concern involves the divergence between private and social costs and benefits, known variously as economic externalities or spillovers, which emerge from both public and private resource development decisions. A fragmented approach to management and a failure to adequately incorporate externalities into the accounts of development decisions are considered to be contributing factors in the misallocation of coastal resources.

In examining the incidence of resource use conflicts, the authors note that "the largest metropolitan areas in the United States are located in the coastal zone." It is in these areas that the competition of alternative resource uses is most acute. Housing and commercial development, for example, is regarded to have a negative impact on the productivity of the coastal zone habitat for fish. As a result, conflicts arise between private "developers" whose interests include the construction of houses (habitat for people), and government fish and wildlife agencies, whose responsibilities include environmental protection. To the extent that people have a right to live in the coastal zone, the central issue is that of mitigating the negative spillovers that result from the intrusion of human population on the "natural" environment.

In providing a perspective of the requirements to allocate coastal resources efficiently and equitably, an interdisciplinary approach to management is articulated. To the extent that a market system permits an optimal allocation of resources from the point of view of efficiency, the authors indicate that government should develop policies that permit private sector involvement in the allocation of resources. However, where market deficiencies, such as externalities, inhibit the proper functioning of the market, there is a requirement for government corrective action. The legal system provides a basis for corrective action from a legal perspective of public and private interests in property. The principal legal approach presently used in the management of coastal resources is through legislation designed to eliminate externalities.

The political system also plays an important role in the allocation of resources through an interest in income redistribution and through direct intervention in the operation of the market. The rationale for political intervention has generally been based on market deficiencies. And, on the basis of this rationale, numerous levels of government agencies have become involved in the management of coastal resources to the point that coordination of efforts is difficult if not impossible. The authors indicate that a proliferation of management agencies has the potential to add to the cost of resource allocation, which can lead to a suboptimal allocation of resources. There is also the danger of allocating resources to the most efficiently organized interest groups. In this regard, an interest is expressed in the allocation of resources on the basis of merit rather than on the basis of politics.

Resource management requires a delineation of the division of labor between the public and private sectors. Governments' role should be to identify externalities and seek "market-oriented distribution systems" to eliminate market deficiencies. In articulating private infringements on public rights, governments have a responsibility to designate a cure but not necessarily manage the cure. The private sector, in acknowledging property rights must be permitted to allocate resources according to market efficiency objectives, and to play a responsible, significant role in the merger of the market and the bureaucracy.

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(R186)

Agricultural Engineering. *Frederick W. Wheaton. John Wiley and Sons, New York, Chichester, Brisbane, and Toronto. 1977. xx + 708 p. $36.00.*

The biologically bent aquaculturist has often depended on insight and in many instances trial and error in the design and construction of rearing facilities. Although he is usually aware that specific technical information most probably exists somewhere, an exhaustive literature search usually turns up reams of equations that are only marginally pertinent to his application or even worse the promising reference on biological filters ends up being more appropriate to germ warfare than aquatic production. Thanks to the existence of this book, which gathers together relevant information from fields as diverse as ship building and sewerage, the biologist is now armed with the basic principles in a sufficiently comprehensive form to enable him to either obtain or construct the necessary equipment to do the job.

The first six chapters provide an overview of aquaculture in the world, followed by a description of the physical chemistry of water, and concludes with chapters dealing with oceanography, hydrography, and ecology of natural bodies of water. These introductory chapters should be especially useful for engineers getting their feet wet for the first time in aquaculture. The remaining eight chapters describe the design characteristics of equipment and the principles involved in manipulating water (pipes, pumps, ponds, impoundments, filtration, disinfection, aeration, and recirculation). Fortunately, the author does not become preoccupied with simply presenting diagrams of the various commercial models available, but instead provides the reader with an understanding of operational principles as well as the limitations, so that much of the installations can be performed at the appropriate scale.

Because the book transcends several traditional disciplines it is bound to create a few difficulties when read from cover to cover. While the biologist will be scratching his head over the performance characteristics of various centrifugal pumps in chapter 11, the uninitiated engineer will no doubt ponder over the concept of gross conversion efficiency as it relates to the feeding of fish in chapter 3.

Minor criticism might be extended to the limited treatment given to floating fish pen construction, mooring techniques, and methods of controlling fouling. The principles of degassing supersaturated water as opposed to aeration might have received some attention. The problems of electrolysis of metals in seawater and the application of solar collectors, heat pumps, heat exchangers from the point of view of conservation, and obtaining low grade waste heat from industrial sources might have also been considered.

The field of aquacultural engineering is relatively new and the reader should not expect to find instant engineering solutions to all his problems from this book. What he will discover, however, is how other fields of technology have dealt with similar problems along with a very good list of references to get him on his way.

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Pollutant Effects on Marine Organisms. *Edited by C. S. Giam. Lexington Books, D.C. Heath and Co., Lexington, Mass. 1977. xi + 213 p. $17.00 U.S.*

This book summarizes the proceedings of a workshop held in May 1976, to discuss ongoing research and to identify research priorities in the effects of pollutants on marine biota. The book is in two sections: the first is a list of recommended research priorities with some discussion of the factors that led to their compilation, and the second (and by far the larger section) consists of abstracts of 18 papers presented at the meeting, nine of which are subsequently printed in full. The book is well produced, and I noticed only a few typographical errors.

I found the first section of the book, "Workshop recommendations for future research," interesting. The recommendations have been divided somewhat arbitrarily into those dealing with chemistry (identification and estimation of pollutants); biochemistry (ability of marine biota to accumulate, modify, and clear pollutants); physiology (effects of pollutants on organisms), and research systems (integrated approaches to studies in previously mentioned areas). The recommendations for chemical and biochemical work are quite specific, and generally involve acquisition of more data and information using established approaches. In contrast, recommendations for physiological work, although thoughtful, are much more vague and reflect the fact that we know much more about chemical behavior than about the biological effects of marine contaminants. The recommendations were drawn up 3 years ago, but the priorities have not changed much since then, although some of the details might be slightly modified. In general, the section provides a concise summary of the problems in this field.

I found the second section of the book (abstracts and papers presented at the meeting) less satisfactory. I do not know how the nine papers printed were selected from the 18 abstracts listed; four of the papers deal mainly with petroleum hydrocarbons, three mainly with metals, one with chlorinated hydrocarbons and phthalates, and one with general direction and research priorities. This selection reflects fairly accurately the abstracts of the presentations, but I question whether it reflects current problems of marine pollution research. I thought also that the papers illustrated a rather conventional approach to the problems of marine pollution; six of them were oriented toward specific toxicants (e.g. the effects of pollutant "A" on system "B") and only two approached the problem of investigating more general responses to chemical stress. Most of the papers are "primary" documents, and although individually good (as far as I can judge), they focus on more specific and more scattered topics than is suggested by the rather general title of the book.

I do not know what kind of reader will use this book. The general reader, or the newcomer to the field of marine pollution, would find the recommendations for research (and the background to them) useful, but the choice and content of the papers may be too scattered and specific to provide an overview of the field. On the other hand, the specialist in the field will probably find that much of the background material and the recommendations is familiar and that some of the material presented in the papers may already be available in the primary literature.

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Planning of Aquaculture Development — An Introductory Guide. *T. V. R. Pillay. FAO — Fishing News Books Ltd., Farnham, Surrey, England. 1977. 71 p. £4.80.*

In July 1974 a meeting of selected aquaculture experts was jointly sponsored by FAO and the Svanøy Foundation of Norway to discuss "Strategy for Development of Aquaculture as an Industry." The text of this introductory guide to aquaculture planning was prepared as an outcome of these discussions.

There has been a longstanding requirement in aquaculture for a single document that provides a comprehensive approach to the difficult task of planning aquaculture development on a national or regional scale. This text is too brief to meet that need, but it goes partway by providing the skeletal framework on which an aquaculture development plan can be established. The book will be most helpful to fisheries program administrators and economic planners associated with aquaculture, especially in undeveloped countries, although it should be of more than passing interest to anyone involved in the industry.

All the essential ingredients for a total aquaculture plan are considered, starting from an outline of the background fisheries data required, through levels and patterns of aquaculture development, auxiliary industries, manpower requirements, training, research support, extension services and information, investment decisions, financing, and legal aid measures, and concluding with a section on environmental effects of aquaculture development. The text is written in a crisp, detached style that gets the message across in short chapters providing essential details only. The chapter on Levels and Patterns of Development is the best, giving an excellent comparison of the components and benefits of, and support services required for, small-scale rural aquaculture and a vertically integrated, large-scale industry. The author has emphasized well the extent of government involvement required in aquaculture development, especially in providing support services such as research, financial incentives, etc. Suitable reference is also made to the need for integrating aquaculture development with other fisheries operational and agricultural programs to gain maximum benefits from the experience and organization of these two industries. The chapter on Auxiliary Services does not stand well on its own, and either the content should have been expanded or the information included in another chapter. There are a surprising number of illustrations (26 photos occupying 14 pages) of different aspects of aquaculture in various countries. While they are interesting, they are not referred to in the text and one wonders why they, or at least so many, were included.

My one real criticism is that this text has been published as a book. It is obviously not written as one, and I see no reason in terms of information distribution why its publication as an FAO document would not have been more appropriate. It would not have had its high price tag and thus would be more likely to reach those people who need it.

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(R227)

Books received/Livres reçus[1]

November/novembre 1978

Environmental Chemistry and Cycling Processes. Proceedings of a Symposium held at Augusta, Georgia, April 28–May 1, 1976. *D. C. Adriano and I. Lehr Brisbin Jr. [ed.] Technical Information Center, U.S. Dept. of Energy. 1978. xxxii + 911 p. $15.00 U.S.*

Handbook of Phycological Methods — Physiological and Biochemical Methods. (Sponsored by the Phycological Society of America, Inc.). *Johan A. Hellebust and James S. Craigie [ed.] Cambridge University Press, New York, N.Y. 1978. xiv + 512 p. $29.95 U.S.* (This is the second volume of Phycological Methods, the first volume on Culture Methods and Growth Measurements having been published in 1973.)

3rd Soviet–Swedish Symposium on the Pollution of the Baltic. Ambio Special Report No. 5. *Anders Åkerblom, Ph.D. [ed.] Royal Swedish Academy of Sciences, Stockholm. (North American Distributor: Columbia University Press, Irvington-on-Hudson, N.Y.) 1978. 294 p. $25.00 U.S. (paper).* (All the papers in the Report are in English, with Russian Abstracts).

*__The__ *Selenastrum capricornutum* **Printz Algal Assay Bottle Test: Experimental Design, Application, and Data Interpretation Protocol.** *William E. Miller, Joseph C. Greene and Tamotsu Shiroyama. Corvallis Environmental Research Laboratory, U.S. Environmental Protection Agency, Corvallis, Oreg. 1978. vi + 126 p. No Charge.* (This manual is an update on the Laboratory's 1971 publication, and forms the basis for the phytoplankton section in the 15th edition of "Standard Methods for the Examination of Water and Wastewater.")

December/décembre 1978

*__Anatomie de__ *Latimeria chalumnae*. *Tome III. Appareil digestif — Appareil respiratoire — Appareil urogénital — Glandes endocrines — Appareil circulatoire — Téguments — Ecailles — Conclusions générales. Rédacteurs J. Millot, J. Anthony et D. Robineau. Editions du Centre National de la Recherche Scientifique, Paris. 1978, 198 p. + LXXXVI plates (36 p.) p. 450.00Fr. F.* (Traite des appareils digestif, respiratoire, urogénital, endocrine et circulatoire, ainsi que de la peau et des écailles; résume et donne les conclusions générales découlant du présent volume et des deux volumes précédents./Deals with the digestive, respiratory, urogenital, endocrine, and circulatory systems, and skin and scales; summarizes and gives general conclusions from this and the previous two volumes.)

Underwater Photography for Everyone. *Flip Schulke. Prentice-Hall, Inc., Englewood Cliffs, N.J. 1978. xv + 219 p. $17.95.* (A profusely illustrated book, covering most aspects of underwater photography from very simple to very complex.)

Recreational Freshwater Fisheries. Their Conservation, Management and Development. *A Water Research Centre Conference (Medmenham Laboratory, Medmenham, Bucks, England). John S. Alabaster [ed.] 1978. xvii + 312 p. £10.00.* (The Proceedings consists of 19 papers and four summary reports of discussions on the various topics.)

Pelagic and Semi-Pelagic Trawling Gear. *John Garner. Fishing News Books Ltd., Farnham, Surrey, England. 1978. 60 p. £9.00.* (This is a companion book to the author's Modern Deep Sea Trawling Gear (R-206) and David Thomson's Pair Trawling and Pair Seining (R-229), by the same publisher.)

[1] Entries in this list *not* marked by an asterisk are available for review by interested readers for a 3-month period from the time of publication of the list. For information, please write to

[1] Les ouvrages inclus dans cette liste et *non* accompagnés d'un astérisque peuvent être mis à la disposition de lecteurs intéressés qui voudraient en faire l'analyse, et ce, pour une période de 3 mois à compter de la date de parution de la liste. Pour plus de renseignements, veuillez écrire à

David P. Scott
Department of Fisheries and Oceans
Freshwater Institute
501 University Crescent
Winnipeg, Man. R3T 2N6

COMING NEXT MONTH / À PARAÎTRE LE MOIS PROCHAIN

Sorption of cadmium and its effect on growth and the utilization of inorganic carbon and phosphorus of two freshwater diatoms **H. L. Conway and S. C. Williams**

Short-term covariability of chlorophyll and temperature in the St. Lawrence Estuary **S. Demers, P. E. Lafleur, L. Legendre, and C. L. Trump**

Infectious pancreatic necrosis virus: quantification of carriers in Lake populations during a 6-year period **T. Yamamoto and J. Kilistoff**

Quantification of vitellogenin in Atlantic salmon (*Salmo salar*) plasma by radioimmunoassay **D. R. Idler, S. J. Hwang, and L. W. Crim**

Population-genetic study of the effects of selective fishing on the growth rate of trout **L. D. Favro, P. K. Kuo, and J. F. McDonald**

Possible adaptive significance of certain enzyme polymorphisms in steelhead trout (*Salmo gairdneri*) **J. M. Redding and C. B. Schreck**

Predation of sea scallops, *Placopecten magellanicus*, by the rock crab, *Cancer irroratus*, and the American lobster, *Homarus americanus* **R. W. Elner and G. S. Jamieson**

Studies on the sediment of St. Margaret's Bay, Nova Scotia **T. G. Hughes**

Net entanglements of baleen whales in the inshore fishery of Newfoundland **J. S. Perkins and P. C. Beamish**

Detritus and juvenile salmon production in the Nanaimo Estuary: I. Production and feeding rates of juvenile chum salmon (*Oncorhynchus keta*) **M. C. Healey**

Detritus and juvenile salmon production in the Nanaimo Estuary: II. Meiofauna available as food to juvenile chum salmon (*Oncorhynchus keta*) **J. R. Sibert**

Detritus and juvenile salmon production in the Nanaimo Estuary: III. Importance of detrital carbon to the estuarine ecosystem **R. J. Naiman and J. R. Sibert**

Timing and magnitude of energy deposition and loss in the body, liver, and gonads of northern pike (*Esox lucius*) **J. S. Diana and W. C. Mackay**

Notes

Pathogenesis of infectious pancreatic necrosis in Atlantic salmon (*Salmo salar*) **R. N. Swanson and J. H. Gillespie**

Rapid decompression stress accelerates fibrinolysis in fingerling salmon **J. J. Woodward, E. Casillas, L. S. Smith, and B. G. D'Aoust**

ANNOUNCEMENTS / AVIS

Assembly on Current and Future Oceanography

A Public Assembly will be held from September 29 to October 3, 1980 at Woods Hole, Massachusetts, USA, to mark the 50th Anniversary of the Woods Hole Oceanographic Institution.

The Assembly will consist of invited papers on all aspects of oceanography, including scientific, technical, social, and institutional affairs, with particular focus on the future development of these fields.

The Assembly follows the Third International Congress on the History of Oceanography (September 22–26) also to be held in Woods Hole.

For further information contact Dr Peter G. Brewer, Woods Hole Oceanographic Institution, Woods Hole, MA 02543, USA. Telephone (617) 548-1400, Extension 2552.

Assemblée sur l'océanographie présente et future

À l'occasion du 50^{e} anniversaire de fondation de la Woods Hole Oceanographic Institution, il y aura assemblée publique, du 29 septembre au 3 octobre 1980, à Woods Hole dans le Massachusetts, É.-U.

On y présentera des travaux préparés sur invitation sur tous les aspects de l'océanographie, y compris questions scientifiques, techniques, sociales et institutionnelles. On mettra l'accent sur l'expansion future de ces domaines.

L'assemblée suivra le Troisième congrès international sur l'histoire de l'océanographie (22–26 septembre) qui se tiendra également à Woods Hole.

Pour plus amples renseignements veuillez vous adresser à Dr Peter G. Brewer, Woods Hole Oceanographic Institution, Woods Hole, MA 02543, USA. (617) 548-1400, Poste 2552.

SI Units and Symbols

We encourage use of SI units (Système international d'unités) and symbols in the *Journal of the Fisheries Research Board of Canada* for the following list of quantities. A more complete list is given in the *Canada Metric Practice Guide* (CAN3-Z234.1-76) available from the Canadian Standards Association, 178 Rexdale Blvd., Rexdale, Ontario M9W 1R3.

Unités et symboles SI

Nous encourageons l'usage des unités SI (Système international d'unités) et des symboles pour le *Journal de l'office des recherches sur les pêcheries du Canada* pour la liste des quantités ci-dessous. Le *Guide canadien de familiarisation au système métrique* (CAN3-Z234.1-76), que l'on peut se procurer auprès de l'Association canadienne de normalisation, 178, boul. Rexdale, Rexdale (Ontario) M9W 1R3, donne une liste plus complète des unités.

Quantity/Quantité	Name/Nom	Symbol/Symbole
length/longueur	centimetre, kilometre . . ./centimètre, kilomètre . . .	cm, km . . .
area/aire	square centimetre . . ./centimètre carré . . .	cm^2 . . .
volume/volume	millilitre, litre . . ./millilitre, litre . . .	mL, L . . .
time/temps	second/seconde	s
	minute/minute	min
	hour/heure	h
	day/jour	d
frequency/fréquence	hertz/hertz	Hz
mass/masse	gram, kilogram . . ./gramme, kilogramme . . .	g, kg . . .
density/masse volumique	kilogram per cubic metre/kilogramme par mètre cube	kg/m^3
pressure/pression	pascal/pascal	Pa
temperature/température	degree Celsius/degré Celsius	°C
electric current/courant électrique	ampere/ampère	A
conductance/conductance	siemen/siemen	S
luminous intensity/intensité lumineuse	candela/candela	cd
illuminance/éclairement	lux/lux	lx
amount of substance/quantité de matière	mole/mole	mol
molar concentration — volume/molalité concentration — volume	mole per cubic metre/mole par mètre cube	mol/m^3
molar concentration — mass/molalité concentration — massique	mole per kilogram/mole par kilogramme	mol/kg
ppm (parts per million)	microgram per gram/microgramme par gramme	μg/g
	milligram per litre/milligramme par litre	mg/L
	microlitre per litre/microlitre par litre	μL/L
ppb (parts per billion)	nanogram per gram/nanogramme par gramme	ng/g
	microgram per litre/microgramme par litre	μg/L

The following units are not acceptable in the SI and authors using them are asked to give SI equivalents. If both units are given it is preferable to put the non-SI one in parentheses.

Les unités qui suivent ne sont pas acceptées par le SI et les auteurs qui les utilisent sont priés de donner l'équivalent. Si les deux unités sont données, il est préférable de placer entre parenthèses celle qui n'est pas du système SI.

Not acceptable in SI/ Non valides dans le SI	SI equivalents/Equivalents SI	Conversion factors/ Facteurs de conversion
angström/angström (Å)	nanometre/nanomètre (nm)	1 Å = 0.1 nm
micron/micron (μ)	micrometre/micromètre (μm)	1 μ = 1 μm
calorie/calorie (cal)	joule/joule (J)	1 cal = 4.1868 J
inch (in)/pouce (po)	centimetre/centimètre (cm)	1 in/1 po = 2.54 cm
foot (ft)/pied (pi)	metre/mètre (m)	1 ft/1 pi = 0.305 m
mile/mille (mi)	kilometre/kilomètre (km)	1 mi = 1.6 km
curie/curie (Ci)	becquerel/becquerel (Bq)	1 Ci = 37 GBq

MISCELLANEOUS SPECIAL PUBLICATION 39

Food from Water

Fisheries and Aquaculture

Papers presented to the Parliamentary and Scientific Committee at the House of Commons, Ottawa, January 31, 1978.

Contents: Foreword, **F. Maine, M.P.**; Overview, **W. R. Martin**; Main currents in east coast management, **L. M. Dickie**; Great Lakes and other freshwaters, **K. H. Loftus**; Fisheries of the Pacific Region, **Z. Kabata**; Canada's west coast salmon enhancement program — research and development, **C. Groot**; Aquaculture — the farming of fish, **G. I. Pritchard**; Is a governmental monopoly on environmental protection in the interest of Canadians? In the interest of governments? In the interest of environment? **J. R. Vallentyne**; Introduction to the international legal framework for the management and development of world fisheries, **B. I. Applebaum.**

(1978, 32 p., Cat. no. Fs 41-31/39, Free)

Available from

Department of Fisheries and Oceans
Scientific Information and Publications Branch
240 Sparks Street
Ottawa, Canada K1A 0E6

PUBLICATION DIVERSE SPÉCIALE 39

L'eau, source de nourriture

Pêches et Aquiculture

Mémoires présentés au Comité parlementaire et scientifique à la Chambre des communes, Ottawa, le 31 janvier 1978.

Table des matières : Avant-propos, **F. Maine, M.P.**; Tour d'horizon, **W.R. Martin**; Principales tendances dans la gestion de la côte est, **L.M. Dickie**; Les Grand Lacs et autres eaux douces, **K.H. Loftus**; Les pêches de la région du Pacifique, **Z. Kabata**; Programme de mise en valeur des salmonidés de la côte ouest canadienne — recherche et développement, **C. Groot**; Aquiculture — l'élevage du poisson, **G.I. Pritchard**; Le monopole gouvernemental sur la protection de l'environnement est-il dans l'intérêt des Canadiens? Dans l'intérêt des gouvernements? Dans l'intérêt de l'environnement? **J.R. Vallentyne**; Un cadre légal international pour la gestion et l'expansion des pêches mondiales, **B.I. Applebaum.**

(1978, 35 p., N° de cat. Fs 41-31/39F, Gratis)

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240, rue Sparks
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Volume 36, No. 4, April 1979

Volume 36, nº 4, avril 1979

Optimal survey design: lessons from a stratified random sample of macrobenthos **W. Cuff and N. Coleman** 351–361
Two electivity indices for feeding with special reference to zooplankton grazing **H. A. Vanderploeg and D. Scavia** 362–365
Temperature selection and estimated thermal acclimation by rainbow trout (*Salmo gairdneri*) in a thermal plume **S. A. Spigarelli and M. M. Thommes** 366–376
Method, validity, and variability in the age determination of yellowtail rockfish (*Sebastes flavidus*), using otoliths **D. K. Kimura, R. R. Mandapat, and S. L. Oxford** 377–383
Analysis of the British Columbia salmon purse-seine fleet: dynamics of movement **R. Hilborn and M. Ledbetter** 384–391
Selective predation by drift-feeding brown trout (*Salmo trutta*) **N. H. Ringler** 392–403
Sensitivity analysis of two harp seal (*Pagophilus groenlandicus*) population models **R. K. Mohn** 404–410
Correlations between *Daphnia magna* and fathead minnow (*Pimephales promelas*) chronic toxicity values for several classes of test substances **A. W. Maki** 411–421
World distribution of Atlantic salmon, *Salmo salar* **H. R. MacCrimmon and B. L. Gots** 422–457

Notes

A culture technique using marine fish kidney to obtain chromosomes **E. H. Park and S. D. Park** 458–461
In vitro maintenance of amoebocytes from the American oyster (*Crassostrea virginica*) **F. Brewster and B. L. Nicholson** 461–467
Pygmy whitefish, *Prosopium coulteri*, in three lakes of the Copper River System in Alaska **F. H. Bird and K. Roberson** 468–470
Indices of food type preference by a predator **J. E. Paloheimo** 470–473

Book Reviews/Comptes rendus: Coastal resources management (R. B. Ditton, J. L. Seymor, G. C. Swanson) **D. M. Cauvin**; Agricultural engineering (F. W. Wheaton) **A. M. Sutterlin**; Pollutant effects on marine organisms (C. S. Giam [ed.]) **R. F. Addison**; Planning of aquaculture development — an introductory guide (T. V. R. Pillay) **T. G. Carey** 474–476

Books received/Livres reçus 476–477
Coming next month/À paraître le mois prochain 478
Announcements/Avis 479

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